ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 37: 231–256 (2024)
DOI 10.3897/herpetozoa.37.e125965

The herpetofauna of the Sporades Islands (Aegean Sea, Greece): New discoveries and a review of a century of research

Johannes Foufopoulos[1], Stephen Roussos[2], Stamatis Kalogiannis[3], Samuel Kalb[4], Ilias Strachinis[5], Kinsey M. Brock[6,7]

1 School for Environment and Sustainability, Dana Hall, 440 Church St., University of Michigan, Ann Arbor, MI, 48109, USA
2 Department of Biological Sciences, University of North Texas, Denton, Texas 76203, USA
3 Alonnisos, Magnesia, 37005, Greece
4 EA Engineering, Science, and Technology, Inc., 555 University Ave, Ste 182, Sacramento, CA, 95825, USA
5 Department of Genetics, Development and Molecular Biology, School of Biology, Faculty of Natural Sciences, Aristotle University of Thessaloniki, University campus, 54636, Thessaloniki, Greece
6 Department of Biology, San Diego State University, 5500 Campanile Dr, San Diego, CA, 92116, USA
7 Biodiversity Museum, San Diego State University, 5500 Campanile Dr, San Diego, CA, 92116, USA

https://zoobank.org/4FD727DC-7B51-4D54-938E-17C4C531EF2E

Corresponding author: Johannes Foufopoulos (jfoufop@umich.edu)

Academic editor: Günter Gollmann ♦ **Received** 23 April 2024 ♦ **Accepted** 27 June 2024 ♦ **Published** 31 July 2024

Abstract

The Sporades are one of the most biologically important archipelagos in the Aegean Sea (Greece) and have received priority conservation over the last 50 years. However, despite numerous early efforts, its herpetofauna is only partially described, resulting in many distributional gaps that have prevented adequate understanding and management of the resident species communities. We review one century of bibliography from the Northern Sporades and combine this information with a review of museum specimens and insights from numerous extensive field surveys over the last near-decade to provide for the first time a comprehensive picture of the reptiles and amphibians of the archipelago. We report here on 26 new island records and find that the herptile communities of the region are largely derived from the herpetofauna of the nearby Thessaly mainland, with only a few introduced taxa. There is also a small but significant set of endemic taxa in the archipelago. Island species richness declines with decreasing island size and increasing duration of island isolation. Herptile communities on smaller islands are progressively nested subsets of the communities on larger islands. The presence of reptile species depends sensitively on the condition and management of native ecosystems. While non-aquatic species maintain largely healthy populations, most populations are under pressure from the combined effects of rampant tourist development, the destruction and degradation of rare wetland habitats, and the abandonment of traditional agricultural landscapes. We provide recommendations regarding sustainable management of the local reptile and amphibian populations.

Περίληψη

Οι Βόρειες Σποράδες είναι από βιολογικής άποψης ένα από τα σημαντικότερα νησιωτικά συγκροτήματα του Αιγαίου και έχουν τεθεί υπό ιδιαίτερη νομική προστασία εδώ και σχεδόν μισό αιώνα. Ωστόσο, παρά τις πολυάριθμες προσπάθειες, η ερπετοπανίδα της περιοχής δεν έχει μελετηθεί επαρκώς, με αποτέλεσμα να υπάρχουν πολλά κενά στις κατανομές των ειδών τα οποία εμποδίζουν την ολοκληρωμένη κατανόηση καθώς και τη σωστή διαχείριση των βιοκοινωνιών της περιοχής. Εδώ παρατίθεται μια κριτική ανασκόπηση όλης της υπάρχουσας βιβλιογραφίας ενώ ταυτόχρονα έχει γίνει μια εκτενής εξέταση όλων των σημαντικών μουσειακών συλλογών από την περιοχή. Οι πληροφορίες αυτές, σε συνδυασμό με τα αποτελέσματα σχεδόν μιας δεκαετίας έρευνας πεδίου προσφέρουν, για πρώτη φορά, μία ολοκληρωμένη εικόνα των ερπετών και των αμφιβίων του αρχιπελάγους. Η ερπετοπανίδα των νησιών έχει ουσιαστικά θεσσαλική προέλευση και συμπεριλαμβάνει μόνο λίγα ξενικά είδη. Υπάρχει επίσης ένας μικρός αλλά ση-

μαντικός αριθμός από ενδημικά τάξα. Ο αριθμός των ειδών της ερπετοπανίδας ενός νησιού ελαττώνεται με τη μείωση του μεγέθους του νησιού, καθώς και με την αύξηση της διάρκειας απομόνωσης του. Συνεπώς τα ανατολικά νησιά (μετά την Κυρά Παναγιά) έχουν λίγα είδη αλλά και σχετικά υψηλότερο ποσοστο ενδημισμού. Ενώ τα περισσοτερα ήχερσαία είδη διατηρούν σε μεγάλο βαθμό υγιείς πληθυσμούς, όλα τα υδρόβια είδη βρίσκονται υπό πίεση λόγω της έντονης υποβάθμισης και καταστροφής των λίγων υγροτόπων της περιοχής. Η διατήρηση παραδοσιακών αγροτικών δραστηριοτήτων σε συνδυασμό με ικανά επίπεδα βόσκησης ευνοεί τα περισσότερα είδη της ερπετοπανίδας στα μεγάλα νησιά των Σποράδων. Σε αντίθεση, σε μικρές νησίδες η υπερβόσκηση έχει αρνητικές επιδράσεις στα τοπικά είδη. Δίνονται συστάσεις ως προς την ορθολογική διαχείριση των διαφόρων ενδιαιτημάτων του αρχιπελάγους.

Key Words

Amphibia, biodiversity, conservation, Greek islands, herpetofauna, island biogeography, reptilia

Λέξεις-κλειδιά

Αμφίβια, βιοποικιλότητα, διατήρηση, ελληνικά νησιά, ερπτικός, νησιωτική βιογεωγραφία, Ερπετά

Introduction

The Northern Sporades (or simply Sporades) are a chain of islands located off the eastern coast of Thessaly, Greece. They constitute one of the major archipelagos of the Aegean Sea, and have long been recognized for their attractive landscapes and their significance as a biodiversity repository (Kamari et al. 1988; Myers et al. 2000; Iliadou et al. 2020; Konaxis 2020). Though the herpetofauna of the islands has been noted for its richness (Lymberakis et al. 2018), it remains understudied, and the islands' reptile and amphibian communities have never been reviewed in a comprehensive fashion.

The herpetofauna of the Sporades is, from a biogeographic perspective, a fairly coherent assemblage, being primarily affiliated with the nearby eastern Greek mainland, though there is also a notable endemic element. We consider here the main chain of the archipelago, which contains over 45 islands and satellite islets, though only Skiathos, Skopelos, and Alonnisos, the three largest islands, are presently inhabited (Fig. 1). To the southeast of the main Sporades chain is the Skyros cluster, which is located on a separate shelf, and has likely been isolated for a longer period (Dermitzakis 1990). Thus we excluded Skyros and its nearby satellite islets from this study as they are not only comparatively well-known, but also biogeographically distinct, and have been traditionally considered separately (Tiedemann and Mayer 1980; Chondropoulos 1986, 1989; Broggi 2006; Pafilis et al. 2013). The only exception is the island of Piperi, which, despite belonging to the Skyros shelf, is considered here together with the rest of the Sporades due to its immediate geographic proximity and shared management regime as part of a marine protected area.

The herpetofauna of the islands has been shaped strongly by human activities. The islands have a long history of sustained human occupation dating back to the Paleolithic period, with evidence of early activities including animal husbandry and agriculture (Sampson 2006). While human population size and attendant landscape impacts have varied over the millennia as the result of conflict and historical vagaries, it is clear that anthropogenic agro-pastoral activities have been ongoing on the Sporades for millennia (Ginalis 2018). However, the effects of human presence on the local habitats and herptiles have been unevenly distributed across the cluster, with occupation on the smaller islands being much more tenuous and with relatively few impacts beyond religious activities, and small ruminant husbandry (Barouda et al. 2023). In the last century, the ecology of the islands, and the herpetofauna, by extension, have been shaped by three distinct but interacting factors. First, a sustained rural exodus, especially from the smaller islands, has led to the abandonment of the agricultural landscape. Second, the proliferation of mass tourism across the Aegean Basin (Kizos et al. 2007) has had profound impacts on natural habitats, particularly on the western islands. Third, the advance of the modern conservation movement has resulted in the establishment of flagship protected areas in the Sporades (Konaxis 2020). Two Natura 2000 sites lie within the archipelago (GR1430009, GR1430004), with the largest one (GR1430004) constituting the National Marine Park of Alonnisos and Northern Sporades (MPA). The authors are in direct communication with the governmental management team of the MPA, the Ministry of Environment, as well as other NGOs that operate in the Sporades. While the MPA has mainly focused on conservation and protection of marine ecosystems, we expect our work will help in the future direction of conservation, restoration, and further research of the terrestrial ecosystems in the MPA and wider archipelago.

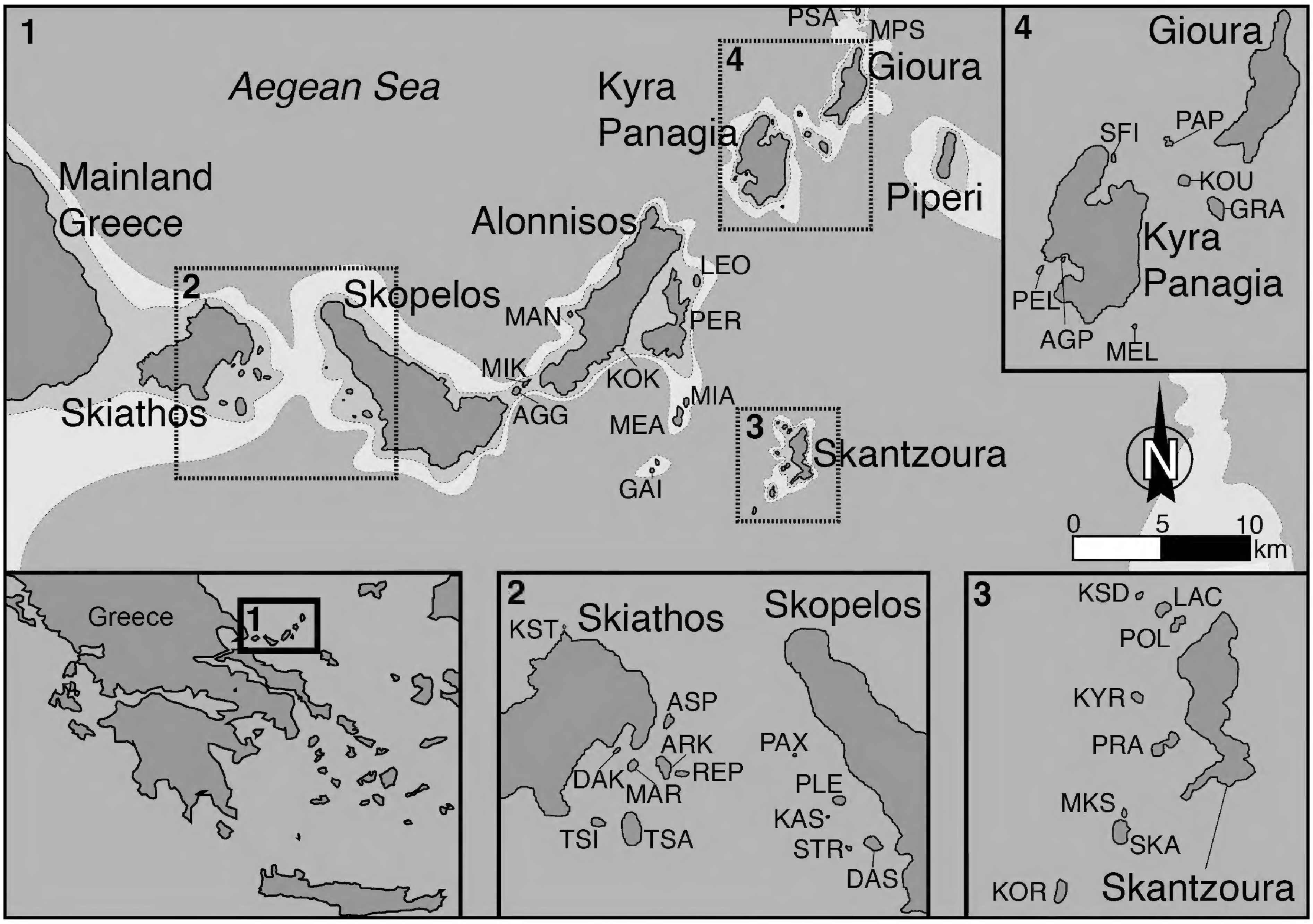

Figure 1. Map of the Sporades study area, including island acronyms. Full faunal information can be found in Tables 1, 2. and additional island information is in Appendix 1: Table A3. Dotted lines surrounding present -day islands indicate 80 m and 120 m isobaths. Light gray/blue indicates land area exposed from approximately 20 kya (at the Last Glacial Maximum) until ca. 14 kya. Light yellow indicates land area that was still exposed at 14 kya but that has become submerged since then (Kalb 2021).

History of herpetological research in the region

The Sporades Islands have had a fairly long history of herpetological field exploration, predominantly by western European scientists. Indeed, up until the very end of the 20th century, herpetological investigations on the islands were almost completely dominated by German-speaking biologists. Commencing in the 1920s and `30s, and through the 1950s, short visits by F. Werner, O. Cyrén, and O.v. Wettstein provided important but limited information on the species communities inhabiting the islands, as well as their basic taxonomic affiliations (Werner 1930, 1938; Cyrén 1935, 1941; Wettstein 1953, 1957a, b, c).

Following these early expeditionary investigations and motivated by the lack of herpetological knowledge in the area, T. Schultze-Westrum and W. Weigand spent extended periods of time on the islands and obtained more fine-grained information on the resident reptiles and amphibians. Their fieldwork, culminating in a substantial series of specimens now residing at the Collection of the Zoological Museum A. Koenig in Bonn, resulted in several foundational publications (Buchholz and Schultze-Westrum 1964; Gruber and Schultze-Westrum 1971; Gruber 1974; Beutler and Gruber 1977; Mayer and Tiedemann 1980) and provided the backbone of herpetological understanding of the Sporades Islands. This basic information was subsequently incorporated into broader-scope review works such as Ondrias (1964), Chondropoulos (1986, 1989), Foufopoulos and Ives (1999), Legakis (2004), Roca et al. (2009), Foufopoulos et al. (2011), etc.

In the last 30 years, however, additional, brief visits by predominantly non-academic herpetologists have resulted in several additional publications, mostly descriptive in nature, that have filled out many knowledge gaps (Bergman 1995; Cattaneo 1997, 1998, 2010; Broggi 2010, 2020; Grano et al. 2013; Passarge 2019; Kalogiannis 2020, 2021). Last but not least, regional-scope laboratory studies utilizing molecular approaches have shed light on the taxonomic affiliations of many of the regional reptile taxa (e.g., Poulakakis et al. 2005; Roussos 2015; Kornilios et al. 2020), though only Poulakakis et al. (2005) explicitly included Sporades samples in the analyses. Consequently, additional molecular studies from the islands are needed, as a fine-grained understanding of the genetic structure and diversity among the reptile populations in the Sporades remains unknown.

This expanding, but relatively disorganized information has created the need for a comprehensive review of the herpetological literature of the archipelago. In this work, we: 1) report on a plethora of new records of species we documented during numerous field trips to the Sporades over the last seven years; 2) review, summarize, and integrate this new information with the existing literature records on the herpetofauna of the region, with the aim of creating a body of information that can be used as a baseline for future studies; 3) provide new field ecology information, as well as conservation and management recommendations for the archipelago's reptile and amphibian communities.

Materials and methods

The Sporades Islands: geology, climate, ecology

The Sporades Islands consist of a diversity of geological substrates, including sedimentary deposits and volcanic rocks. Most of the islands are composed of various forms of limestone, with the exception of Psathoura and Mikropsathoura, which are volcanic in origin (Jacobshagen and Wallbrecher 1984). These fissured and well-draining substrates result in a comparative paucity of surface wetlands with unfavorable effects on amphibians and hydrophilic reptiles. The climate is Mediterranean, characterized by wet winters and warm, dry summers (Iliadou et al. 2020). Though summers in the Sporades can be long and dry, mean annual precipitation is significantly higher and mean annual temperatures are significantly lower than in island groups further south, such as the Cyclades, with important ramifications for the species occurring there (Harris et al. 2020).

From a paleogeographic perspective, most of the western Sporades (west of approximately the 24°E longitude line) are land-bridge islands that were connected to the adjacent Thessalian mainland during the Last Glacial Maximum ~20 kya, when sea levels were about 120 m lower than today (Bintanja et al. 2005). However, even within this continental group, substantial variation exists in the extent of connectivity and insularity throughout the Pliocene and Pleistocene glacial and interglacial periods (Rohling et al. 2014). While Skiathos and its satellite islets have had only a relatively short period of isolation from Thessaly, being connected until 8.5 kya, the rest of the major chain islands (Skopelos, Alonnisos, Mikros Adelphos, and Megalos Adelphos) became separated from the mainland and each other approximately 14–15 kya (Kalb 2021). In contrast, the eastern islands of the main chain (Skantzoura, Kyra Panagia, Gioura, Psathoura, and Piperi) have land bridges submerged below 120 m, and have been isolated for much longer periods of time (> 200 kya) (Kalb 2021).

The natural habitat on the Sporades Islands has been shaped extensively by millennia of human activities. Undisturbed vegetation cover can be relatively dense compared to other, more arid, Aegean islands. The original woodland, likely dominated by *Quercus* sp., was largely reduced and degraded by wood cutting, agricultural activities, and livestock husbandry (Ginalis 2018). As a result, large areas of the main three islands have been converted to a matrix of terraced agricultural slopes, olive groves, and seasonal pasturelands, creating a heterogeneous landscape that is conducive to many typical lowland Mediterranean reptiles and amphibians (Papanastasis et al. 2009; Zakak et al. 2015; Băncilă et al. 2023). Today, in the western Sporades and especially on Skopelos and Skiathos, large areas are also dominated by pine forest (*Pinus* sp.), perhaps due to past forest fires and the abandonment of agricultural areas. In contrast, while vegetation in the eastern Sporades tends to be lower, any relict forest patches consist of Kermes Oaks (*Quercus coccifera*) and Holm Oaks (*Q. ilex*), as pines are absent (with the exception of Piperi). Medium-sized islands support at most tall maquis (dominated by *Juniperus turbinata* on the Skantzoura cluster, *Q. coccifera* everywhere else), while smaller islets, where soils are shallower, support generally only coastal heaths (non-spinose phrygana).

Field visits

We surveyed the herpetofauna of the islands during multiple field expeditions in the period between 2016 and 2024. In addition, one of the authors (SK) lives on the islands and has been conducting impromptu herpetological searches for several years. We used both diurnal and nocturnal surveys, covering all major vegetation types, as well as a variety of distinct microhabitats across the whole archipelago. Whenever possible, we document new records with specimens or photographs, which we have deposited in official museum collections. Beyond ecological and presence data, we also collected information on local reptile names (see Appendix 1: Table A2). All islands of the archipelago were visited, often numerous times, with only 5 islets not visited to date (Gaidaronisi, Manolas, Mikroskandili, Lachanou, and Kassidis). All visited islands harbored at least one species of reptile, with the exception of Kastronisia, a small islet near Skiathos where no reptiles were detected. See Appendix 1: Table A3 for a list of both official and alternative island names.

Results

Island diversity, endemism, and abundance

We summarize our findings as well as past findings on species occurrences in Tables 1, 2. Species richness decreases across the archipelago (Fig. 2), from the youngest to the oldest islands with regards to insularity, and from the largest to the smallest islands in terms of area. Since the archipelago is a chain of islands, and submerged land bridges get deeper towards the more terminal end of the chain in the east, decreasing richness generally follows

a west-to-east geographic pattern, as the oldest islands to the east have probably experienced more species extinctions over their longer period of isolation. Subspecific taxa of lizards (e.g., *P. erhardii ruthveni*, *M. kotschyi fuchsi*) have been described from this archipelago based on morphology, and these taxa are more frequently represented on the smallest Sporades islands, resulting in higher percent endemism on the smallest islets (Fig. 3).

Squamates are the most speciose group in the Sporades, with eight lizard and eight snake species. The most widespread lizard species are Kotschyi's gecko (*M. kotschyi* – 30 islands) and the Aegean wall lizard (*P. erhardii* – 40 islands). Lizards with the most limited distributions in the Sporades are the Skyros wall lizard (*P. gaigeae* – 1 island) and the European glass lizard (*P. apodus* – 2 islands). The most widely spread snake species are the Caspian whipsnake (*D. caspius* – 5 islands), the nose-horned viper (*V. ammodytes* – 5 islands), and the four-lined rat snake (*E. quatuorlineata* – 5 islands). The snake species with the most limited distributions in the Sporades are the cat-eyed snake (*T. fallax* – recorded only from Alonnisos, Skopelos, and Peristera), the Balkan whipsnake (*H. gemonensis* – only recorded from Tsougria and Aspronisi), the Eastern Montpellier snake (*M. insignitus* – recorded from Skiathos and Skopelos), and Dahl's

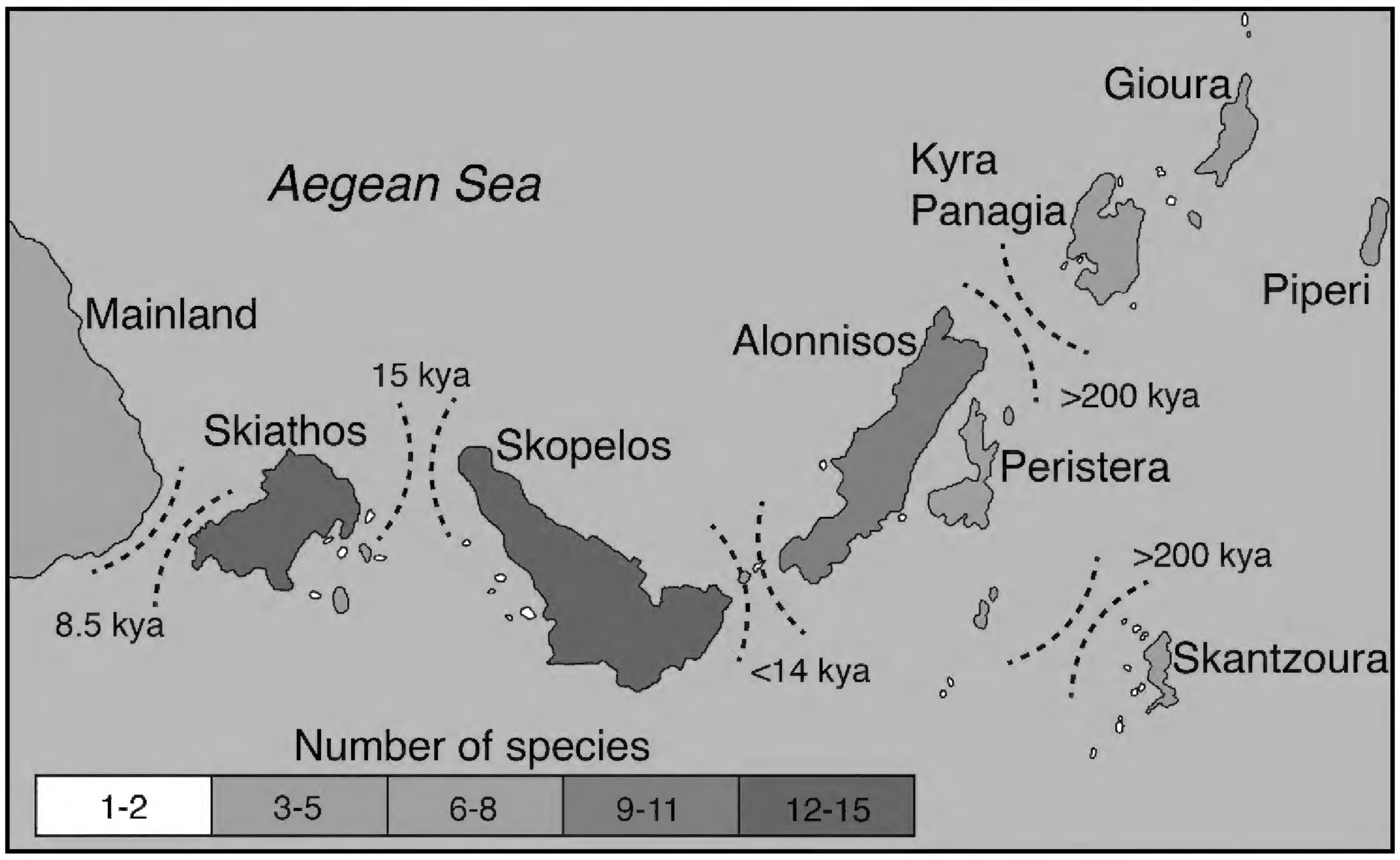

Figure 2. Species richness in the Sporades. Color represents the number of species found on an island. The number of species per island decreases with island size. Species richness also declines from west to east as the duration of island isolation increases.

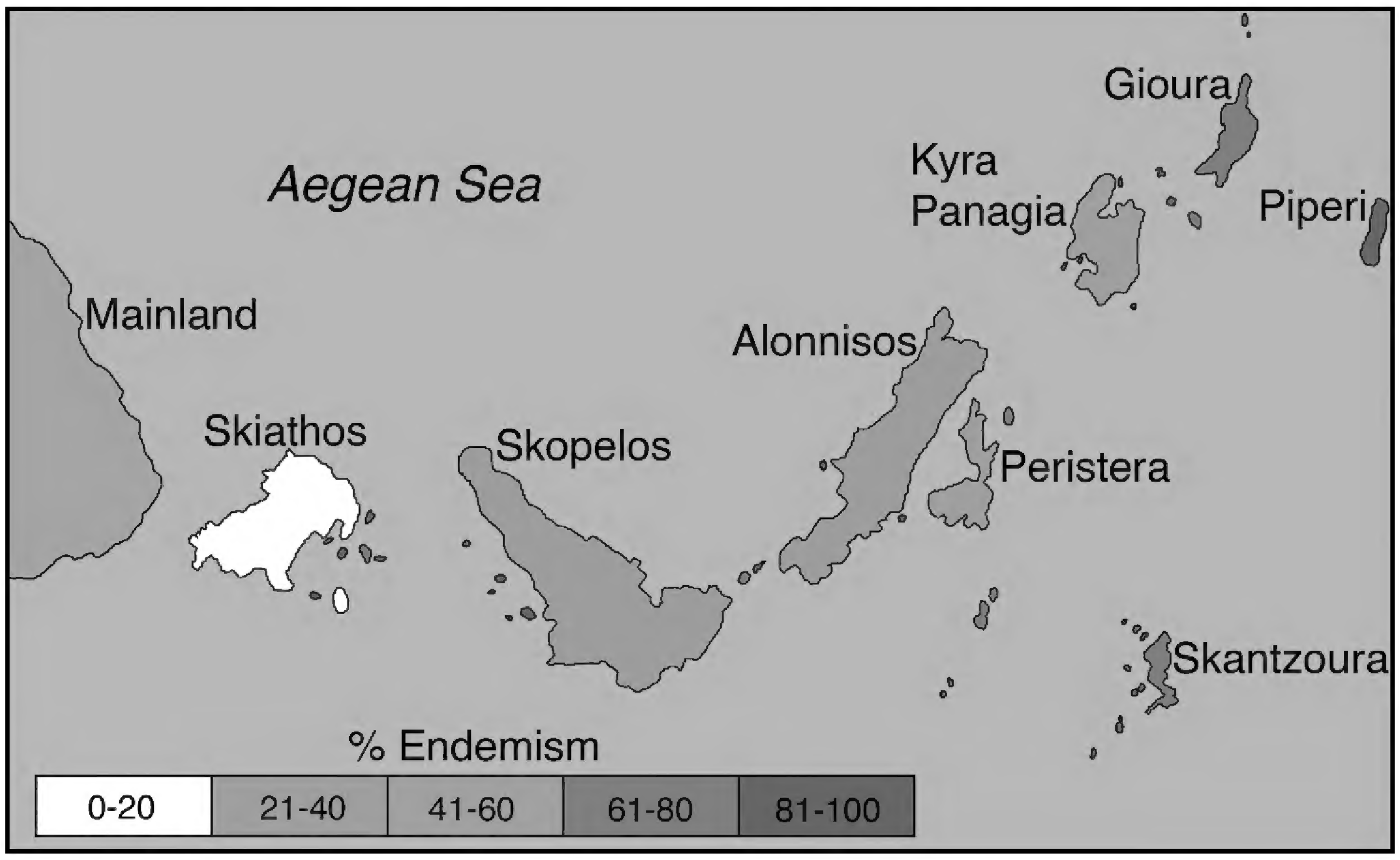

Figure 3. Levels of island endemism of the herpetofauna in the Sporades, expressed as the number of endemic taxa relative to the total number of species on an island (endemic is defined here as any island lineage described as discrete in the taxonomic literature at either the species or the subspecies level, e.g., *P. gaigeae*, *P. erhardii ruthveni*, *M. kotschyi fuchsi*). Older and more isolated islands (on the eastern end of the Sporades chain) have a stronger endemic element. Smaller islands also have high endemism scores, likely because relatively hostile conditions allow only for the persistence of old, locally-evolved taxa.

whipsnake (*P. najadum* – only recorded from Skiathos). Overall, there appear to be some checkerboard distributions of snakes across the Sporades suggestive of competitive intraspecific relationships. Amphibians and turtles are the least common groups of herpetofauna in the Sporades and are most at risk of local extinction due to habitat loss across the archipelago. Amphibians occur only on the young, westernmost large islands of Skiathos and Skopelos, where they are relatively abundant near surface waters. Though anapsids occur on the four largest islands, they are the rarest group of herpetofauna in the Sporades, and terrapins are declining as crucial wetland habitat disappears.

Species accounts

Amphibians

Amphibians have a marginal presence on the islands, with only three species from three families (Bufonidae, Hylidae, and Ranidae) historically recorded from the three largest Sporades (Skiathos, Skopelos, and Alonnisos). However, all amphibians are now likely extinct from Alonnisos, and their future on Skiathos and Skopelos is uncertain. Despite years of searching, we have no new records to report for amphibians.

***Bufotes viridis*, green toad (Laurenti, 1768)**

The green toad is known only from Skopelos, where it was first reported by Werner (1930) and subsequently Cattaneo (1998). We made several observations of this species in the eastern part of Skopelos, often somewhat close to inhabited places (e.g., near the main town and around the meadows of Staphylos), where there is standing or flowing water in the form of wells, flooded fields, and canals. Adults were very active on warm, humid nights during the breeding period. The largest count of individuals was made on 25th March 2022, at 19:40 h, with an air temperature of 16 °C, when about 100 calling males were observed in a flooded field near Staphylos. During a visit to the same spot in April 2023, the fields were completely dry, and only a few calls were heard in the distance. Roadkilled individuals were also frequent on the main road crossing the agricultural plain of Staphylos, south of Skopelos town, and a few adults were found under stones in the same area. Despite the seemingly healthy population on Skopelos, toads are largely dependent on the few suitable breeding spots scattered in a handful of degraded locations that are heavily influenced by human activity and are therefore under the threat of decline.

***Hyla arborea*, European tree-frog (Linnaeus, 1758)**

We confirm the presence of the European tree-frog, *Hyla arborea*, on Skiathos. Until now, this species was only reported by Cattaneo (1997), who discovered a single roadkilled individual. We found the European tree-frog to be common on Skiathos, where it is widespread across the island and mainly inhabits humid, lowland habitats such as slow-flowing streams and their estuaries, flooded fields, vernal pools, and marshes. Particularly dense populations also breed in man-made structures such as abandoned swimming pools, fountains, and canals around the airport area and in the settlement of Troulos. We heard large choruses in Megalos Aselinos and Vromolimnos during the breeding season, especially after rainfalls when males occupied and called from any form of stagnant water. Reproduction takes place between February and April. It seems that the presence of several swimming pools in inhabited areas has contributed to the large population of this species on Skiathos, since treefrogs possess adhesive toe pads and can easily climb smooth, vertical human-made walls. Despite extensive searching, we cannot confirm a doubtful report with no photo or specimen of *H. arborea* from Alonnisos (Broggi 2010).

***Pelophylax kurtmuelleri*, Balkan marsh frog (Gayda, 1940)**

We confirm the presence of the Balkan marsh frog on Skopelos and Skiathos, where it has also been recorded in the past (Cattaneo 1997, 1998). The marsh frog tends to have a patchy distribution, but can be abundant in suitable habitats. On Skopelos, some individuals were observed in a small seasonal pond located in the Ditropo area and in the coastal marsh of Milia. In Milia, we heard large choruses during spring, and good numbers of the species seem to exist. In the Ditropo pond, which is mostly dry during the warmer months, we observed young froglets during the summer of 2021, indicating successful reproduction. Furthermore, a single adult was seen in a small artificial ditch at the water dam near Panormos. Marsh frogs are more widespread on Skiathos, where we have found them in good numbers in the marsh of Vromolimnos and in the streams in Troulos, Megalos Aselinos, and Lechouni. The stream of Lechouni hosted the largest population recorded so far, with hundreds of individuals of various life stages seen in a single visit. Marsh frogs also used to occur in good numbers on Alonnisos, at least up until the 1980's, but have died out since the late 2000's, most likely due to the loss of breeding habitat. This is evident in several reports by locals who say that frogs were widespread across numerous freshwater springs on the island (Grillitsch and Tiedemann 1984; Broggi 2010). In recent times, the intense exploitation of flowing water used for irrigation purposes on Alonnisos has dried out most of the island's streams. Additionally, the traditional wells and ditches used for agriculture have been replaced by modern ground pumps that can pull significantly more water (Broggi 2010). We detected no evidence of amphibians surviving on Alonnisos despite systematic surveying over several years.

Lizards

Lizards are the most abundant group of herpetofauna in the Sporades. To date, seven lizard species spanning four families have been confirmed in the Sporades:

Ablepharus kitaibelii (Scincidae), *Pseudopus apodus* (Anguidae), *Hemidactylus turcicus*, and *Mediodactylus kotschyi fuchsi* (Gekkonidae), as well as *Lacerta trilineata*, *Podarcis erhardii ruthveni*, and *Podarcis gaigeae* (Lacertidae). We report here on 16 new island records for *M. kotschyi* (12), *H. turcicus* (3), and *P. apodus* (1). Additionally, we report on one ambiguous museum record for *Chalcides ocellatus*.

Ablepharus kitaibelii, snake-eyed skink (Bibron and Bory, 1833)

The snake-eyed skink, *A. kitaibelii*, has a wide distribution across most of the Aegean Sea islands (Chondropoulos 1986). In the Sporades, this species has only been observed on the three larger islands of Skiathos, Skopelos, and Alonnisos (Cyren 1935; Cattaneo 1997; Broggi 2010), and we confirm the presence of *A. kitaibelii* on these islands. During our expeditions, we often found this small, delicate species on the ground in leaf litter, maquis, olive groves, meadows, and especially pine woodlands. We usually encounter *A. kitaibelii* during early morning hours, with overcast conditions, and during the winter, given that its habitat is apt to heat up rapidly during the warmer months. Due to its small size and secrecy, *A. kitaibelii* may seem rare but is actually quite common on Skiathos, Skopelos, and Alonnisos.

Chalcides ocellatus, ocellated skink (Forskål, 1775)

We report here on an earlier, unpublished record of *C. ocellatus* from Skopelos. An adult specimen from the island was deposited in the Natural History Museum of Vienna by a collector (O. Reiser in the 1890s, Voucher Natural History Museum of Vienna 19419/1). However, the species was not mentioned in the travel account, and Reiser's Sporades visit was bookended by visits to other areas of Greece harboring *C. ocellatus*, so doubt exists as to the validity of the record (Reiser 1905). Much of the ocellated skink's contemporary range is the result of historical introductions, generating a discontinuous and patchy distribution (Speybroeck et al. 2016). This species has been found on other Aegean islands, but was likely transported there by humans and successfully established. Despite searching, we have never encountered *C. ocellatus* in the Sporades. Assuming that Reiser's record is not erroneous, and given the long gap since it was observed and the lack of any other specimens or recorded observations of this species in this region, we expect that *C. ocellatus* is not a native species and does not currently occur in the Sporades.

Specimen: Skopelos (NHMW 19419/1).

Pseudopus apodus, European glass lizard (Pallas, 1775)

The only species from the slow -worm family Anguidae found in the Sporades is the European glass lizard. It was first reported by Bergman (1995) on the island of Skiathos, and we report here on a new record of the species from a photograph taken by a citizen on Skopelos (July 2009; Theodora Tsimpo). We can also confirm *P. apodus*' presence on Skiathos, where we observed a few individuals of the species on slopes with dense shrubs in the eastern part of the island. *Pseudopus apodus* is usually found in dense brambles and in grassy areas with some canopy cover on Skiathos (Cattaneo 1997), though this taxon is known to also occupy fairly dry, stony habitats if some vegetation cover is available (Speybroeck et al. 2016). Due to its unique morphology as a legless lizard, this species is difficult to confuse with other herpetofauna in this region.

Photographic voucher: Skopelos (NHMC 80.3.20.52).

Hemidactylus turcicus, Mediterranean house gecko (Linnaeus, 1758)

We report three new island records of the Mediterranean house gecko from Kyra Panagia, Peristera (Fig. 4H), and Arkos. In addition, the species was also recently documented on Piperi (Daftsios et al. 2024). Previously, this species was only known from five islands in the Sporades: the three main islands of Skiathos (Cattaneo 1997), Skopelos (Gruber 1974), and Alonnisos (Grillitsch and Tiedemann 1984), and the small recently uninhabited islands of Tsougria (Grano et al. 2013) off the southeast coast of Skiathos, as well as Pappous near Kyra Panagia (Gruber 1974). We found *H. turcicus* in a variety of warm, rocky habitats, hiding under rocks during the day. It is especially common near areas of human activity and settlements such as buildings, agricultural areas, dry stone walls, piles of rubbish, and ruins. The Mediterranean house gecko originated in the Near East and is considered to have been introduced widely across the warmer areas of the Mediterranean Basin (Moravec et al. 2011). Its distribution in the Sporades maps closely to human habitation, and even among the smaller islets, it occurs only on those with regular human presence. Pappous Islet, for example, was a skete, and Tsougria was settled until the mid -1900s. Even our new record from Arkos is based on an individual found near building materials brought to the island for the construction of a beach bar.

Photographic voucher: Kyra Panagia (NHMC 80.3.87.303), Peristera (NHMC 80.3.87.304).

Mediodactylus kotschyi, Kotschy's gecko (Boettger, 1888)

We report here 12 new island records for Kotschy's gecko, *M. kotschyi*, from the islets of Tsougriaki, Arkos, Daskalonisi, Paximadi, Agios Georgios, Mikronisi, Polemika, Kyrgiagos, Prasso, Skandili, Korakas, Pelerissa, and Piperi (Table 2). Although reliable records of this species are still missing from some islands, this is probably the vertebrate with the widest distribution in the archipelago, being able to survive on small islets with scarcely any vegetation that is otherwise reptile-free (e.g., Daskalonisi by Skiathos or Kassidis and Paximadi by Skopelos). Interestingly, *M. kotschyi* has not yet been

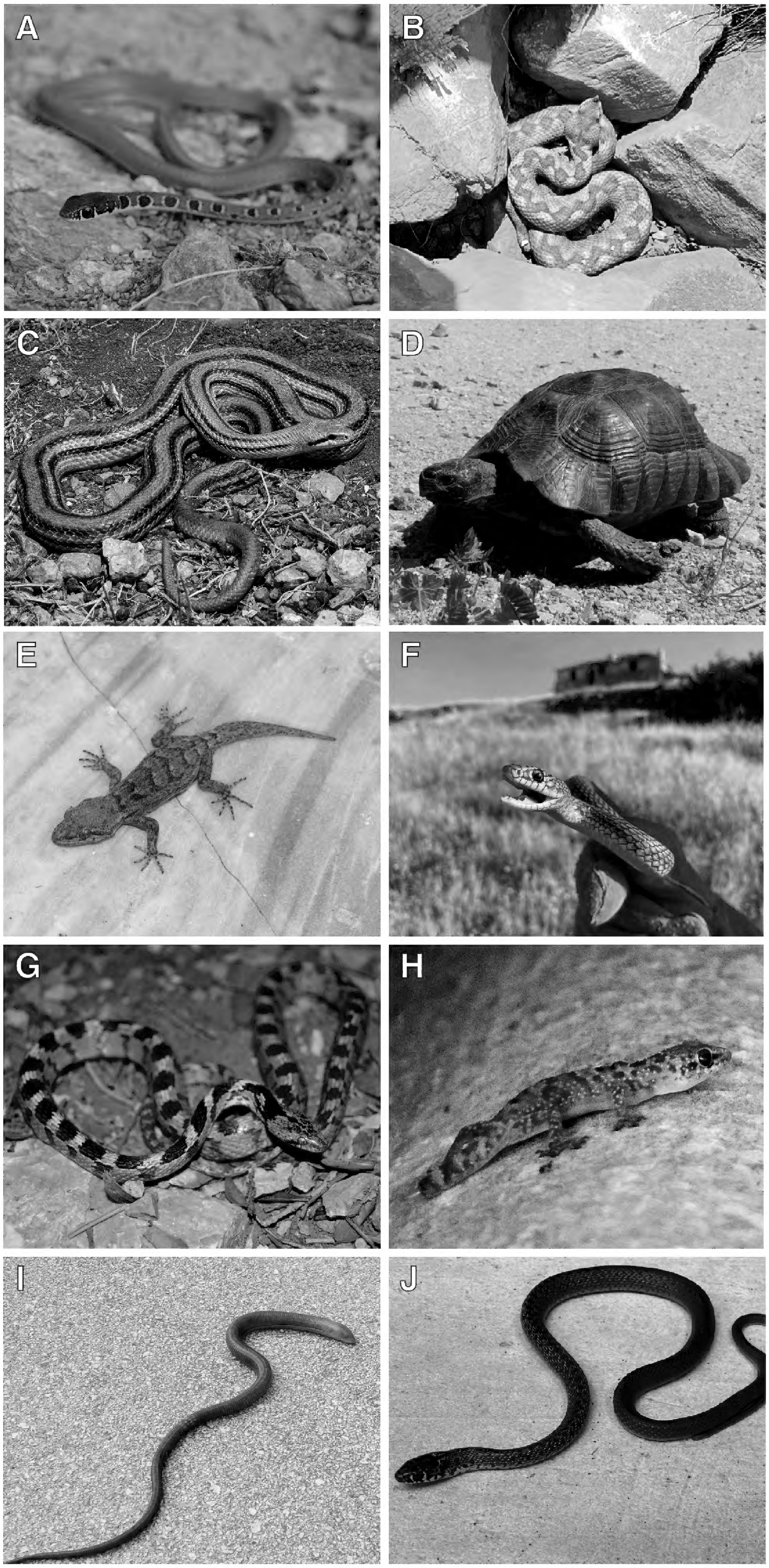

Figure 4. Images of species for which we present new records or newly confirmed occurrences. **A.** *Platyceps najadum* from Skiathos; **B.** *Vipera ammodytes* from Peristera; **C.** *Elaphe quatuorlineata* from Gioura; **D.** *Testudo marginata* from Skopelos; **E.** *Mediodactylus kotschyi* from Skandili; **F.** *Dolichophis caspius* from Skantzoura; **G.** *Telescopus fallax* from Alonnisos; **H.** *Hemidactylus turcicus* from Peristera; **I.** *Pseudopus apodus* from Skopelos; **J.** *Hierophis gemonensis* from Tsougria.

found on Skiathos itself, perhaps because of the dense vegetation and plethora of water, or some other ecological or historical factor. This species has an irregular distribution across the Aegean and is relatively rare on the mainland, and Skiathos is more mainland-like than the rest of the Sporades.

Kotschy's gecko is a small Palearctic "naked-toed" gecko (Beutler 1981). It is easily recognized by its gray coloration, dark chevron dorsal patterning, and thin, kinked toes that lack adhesive toe pads (see Fig. 4E). The populations of most Sporades islands have been taxonomically assigned to *M. kotschyi fuchsi*, which is morphologically distinct from the mainland *M. k. bibroni*. This taxon can be distinguished by the general lack of preanal pores (an average of 0.6 in *M. k. fuchsi* versus 3.8 in *M. k. bibroni*); the larger number of ventral scale rows (an average of 35.8 in *M. k. fuchsi* versus 24 in *M. k. bibroni*); and the larger number of separate tubercles on the hind thigh (an average of 6 in *M. k. fuchsi* versus 3.4 in *M. k. bibroni*) (see Beutler and Gruber 1977; Beutler 1981 for further morphological details). *Mediodactylus k. fuchsi* is an island endemic that is restricted to the eastern Sporades islands up to, and including, the Alonnisos cluster. The remaining populations, Skopelos and westward, are considered by Beutler and Gruber (1977) to be transitional to the mainland *M. k. bibroni*. Beyond these lineages, the populations from the extralimital Skyros archipelago have been assigned to *M. k. schultzewestrumi* (Beutler and Gruber 1977). The taxonomic affiliation of the intermediate Piperi population remains to be determined. While these subspecies have been described based primarily on morphology, it is not clear whether they will hold up in a more holistic species delimitation framework that incorporates molecular data. Prior studies that have inferred evolutionary relationships with one or a few genes have synonymized many subspecies in the Aegean islands to the species *M. kotschyi* from the European continental shelf (Kasapidis et al. 2005; Kotsakiozi et al. 2018).

While Kotschy's gecko is primarily crepuscular, we commonly encountered it basking on rocks, stone walls, or trees in the first hours of the morning sun and last hours of daylight, even during the hot summer months. This species favors dry, rocky habitats and can reach high densities on dry stone walls, though we also observed *M. kotschyi* on trees and wooden telephone poles. On smaller, uninhabited, predator-free islets, it is more typically encountered low to the ground under rocks or debris. Our observations suggest that the density of this species is inversely proportional to the size of the island, achieving the highest densities on small rocky islets. This may be both the result of island competitive release, as well as susceptibility to predation on larger islands (Itescu et al. 2017).

Specimens: Tsougriaki (NHMC 80.3.85.1970), Mikros Adelphos (NHMC 80.3.85.1971-1972), Skantzoura (NHMC 80.3.85.1973-1975), Prasso (NHMC 80.3.85.1976-1979), Kyra Panagia (NHMC 80.3.85.1980-1981), Gioura (NHMC 80.3.85.1982-1984), Grammeza (NHMC 80.3.85.1985)

Photographic voucher: Skandili (NHMC 80.3.85.2012), Korakas (NHMC 80.3.85.2011).

Lacerta trilineata, Balkan green lizard (Bedriaga, 1886)

The Balkan green lizard occurs on the three largest and westernmost islands of the Sporades, as well as on two uninhabited Skiathos satellite islets: Tsougria and Arkos. In 1938, Werner claimed that he observed both *Lacerta trilineata* and *L. viridis* on Skiathos (Werner 1938). However, no observations of *L. viridis* have been reported since, and at present it is considered an erroneous observation. We have no new records of *Lacerta* to report from our expeditions, and we confirm the presence of *L. trilineata* on Skiathos, Skopelos, Alonnisos, Tsougria, and Arkos.

Adult *L. trilineata* from the Sporades has a vivid, bright green coloration that can be speckled with black or bright blue scales. Individuals from Skiathos are noticeably smaller and seem to have a slenderer head than adults from the mainland, Skopelos, and Alonnisos. The typical throat color we observed on the islands is bright yellow, but in some males, a small area of the throat is light blue. Additionally, adult *L. trilineata* have dramatically different coloration than juveniles, the latter of which have light grey/brown dorsal coloration often with three bright pale-yellow lines running in parallel down the dorsum, though about 4/5 of juveniles in the Sporades have the uniform morph, as based on 100s of field observations by us and noted by others (Cattaneo 1997). Adults can be difficult to find, as they generally escape quickly into dense vegetation when approached by humans. Typically, we found this species basking or climbing high up on shrubs, reeds, and stonewalls. *Lacerta trilineata* is exceptionally common on Skiathos, where it is the most abundant lizard species and is found in virtually all habitat types. Fewer observations were made on Skopelos and Alonnisos, mostly from agricultural areas and olive groves.

Podarcis erhardii, Aegean wall lizard (Bedriaga, 1882)

The Aegean wall lizard is, together with Kotschy's gecko, the most abundant reptile in the Sporades (Kalogiannis 2020) and occurs on at least 40 islands in the region. We have no new records to report for *P. erhardii*, despite searching islands like Tsougria and Kastronisia, where we would expect to find wall lizards despite the previous lack of records. The only islands where *P. erhardii* has not been observed, and is presumed absent, are Tsougria, the Kastronisia islets, Daskalonisi, Paximadi, Kassidis, and Piperi. Furthermore, we were not able to confirm the species on Skiathos, despite a past record by Bergman (1995), likely of a marginal population of introduced individuals. Notably, this species is absent from Piperi, where it is replaced by an endemic subspecies of the Skyros wall lizard, *P. gaigeae weigandi* (Gruber and Schultze-Westrum 1971). Though many subspecies of *P. erhardii* have been described from the Aegean Sea,

only *P. e. ruthveni* (Werner 1930) is presently recognized in the Sporades (see Gruber 1986 for discussion). *Podarcis e. ruthveni* can be distinguished from mainland *P. e. riveti* based on dorsal scalation, as *P. e. ruthveni* has more dorsal scales than *P. e. riveti*. In the Sporades, *P. erhardii* is phenotypically variable, both within and between islands (Cyren 1941).

Few studies have quantitatively assessed morphological variability between island populations of wall lizards in the Sporades, though we confirm here some patterns that have been noted by others prior (Cyrén 1941; Gruber and Schultze-Westrum 1971). Morphologically, wall lizards from Skopelos were relatively small and had the longest legs, while lizards from the easternmost islands were larger and had shorter, more stout legs. This species also varies considerably in dorsal coloration from island to island. Lizards from the western islands tend to be brown, while lizards from the eastern islands are dusky gray-green (Fig. 5). Thus, with progressive distance from the mainland, lizards get larger, darker, more stout, and have fewer scales, especially east of the 24°E longitude line, marking the "old" islands located off the continental shelf. Cyrén (1941) also noted a similar pattern and found a morphological distinction between the older island populations east of the line and the western populations encapsulated under the presently defunct subspecies *psathurensis* vrs. *skopelensis*. Gruber and Schultze Westrum (1971) note that *P. erhardii* has on-average larger body sizes on smaller rather than on larger islands, presumably because of marine subsidies (Stadler et al. 2023). Only the very smallest rock islets without substantial seabirds are exceptions to this rule (e.g., Mikroskandli). Colorwise, we noticed a tendency for *P. e. ruthveni* to follow the general substrate pattern, with lighter -colored animals on limestone and relatively darker ones on dark, volcanic substrate, like on the easternmost islands of Psathoura and Mikropsathoura. We observed larger blue and aquamarine dorsolateral color patches on small island lizards. The venter of individuals is typically one-colored throughout the archipelago, ranging from dirty white to yellowish, orange, and reddish on Kokkinonisi (a small island across from the Kokkinokastro peninsula of Alonnisos). This lizard species has polymorphic throat coloration, and individuals can be either orange, yellow, white, or a mosaic combination of two of these colors (Brock et al. 2020). Based on our observations, white -throated morphs are by far the most common on every island in the Sporades. With the exception of Alonnisos, we only found orange, white, and mosaic orange-white individuals during our expeditions and note that these are the only throat color morphs currently documented in georeferenced photographs on iNaturalist (www.inaturalist.org), suggesting that the yellow throated morph is largely absent from this region.

Like other species of *Podarcis*, *P. e. ruthveni* is an ecological generalist and can occur in almost any habitat in the Sporades, including agricultural and urban areas. As its common name suggests, we frequently find this lizard in high densities on dry stone walls characteristic of the region, and it can thrive around humans unless feral cats are present (Krawczyk et al. 2019).

Schultze-Westrum and others note that all islands in this region that sustain the shrub *Pistacia lentiscus* are inhabited by *P. erhardii* (Buchholz and Schultze-Westrum 1964; Gruber and Schultze-Westrum 1971), and even refer to it as a 'true bush lizard' ('richtiggehende Buscheidechse'). We agree that it achieves the highest densities in relatively open habitat with *P. lentiscus*, which provides cover without completely shading out the ground as *Pinus* forest does. Distributional data also suggest that in the absence of anthropogenic refugia, the species can be susceptible to the presence of diurnal snake predators. For example, *P. erhardii* is absent from Tsougria while occurring on neighboring Tsougriaki (aka Mikrotsougria), perhaps because of the presence of *H. gemonensis*, which is an effective *Podarcis* predator (Speybroeck et al. 2021). This effect may be exacerbated by competition by the syntopic *Lacerta*, which, by virtue of its size, is not as susceptible to *H. gemonensis* predation.

On small, uninhabited islands, we usually find this species basking on rocks or under larger, evergreen shrubs and other vegetation during the heat of the day. Notably, this species was extremely common on every island it was found on, even on the smallest uninhabited islands with very few resources. As small-bodied secondary consumers, these lizards play an important ecological role as they eat and are eaten by a variety of animals. On the Sporades, the species harbors relatively simple generalist parasitic helminth communities, the complexity of which declines with island area (Roca et al. 2009). Though wall lizards are primarily insectivorous, they can thrive on tiny islands due to their flexible diets that include plant material, large venomous arthropods, and other conspecifics (Brock et al. 2014; Madden and Brock 2018; Patharkar et al. 2022). On some islands like Strongyllo (or Kyriagos [near Skantzoura]), these lizards are associated with *Falco eleonorae* nests and appear to feed on falcon prey leftovers (Schultze-Westrum 1961). Lizards from small islands appear to be more inquisitive, have shorter flight initiation distances, and appear also to be slower runners than on the larger islands, similar to *P. erhardii* in the Cyclades (Brock et al. 2015; Semegen 2018). Additionally, a recent study found that average clutch size varies considerably between island populations proportionally to the number of predators, ranging from a minimum of 1.6 eggs on Mikropsathoura to a maximum of 2.6 eggs on Skopelos (Foufopoulos et al. 2023).

Specimens: Tsougriaki (NHMC 80.3.51.2981-2982), Agios Petros (NHMC 80.3.51.2983-2984), Grammeza (NHMC 80.3.51.2985-2986), Aspronisi (NHMC 80.3.51.2987-2988), Mikros Adelphos (NHMC 80.3.51.2989), Kyra Panagia (NHMC 80.3.51.2990-2991), Gioura (NHMC 80.3.51.2992-2993), Skatzoura (NHMC 80.3.51.3037).

Figure 5. P*odarcis erhardii ruthveni* from Aspronisi (L) and from Gioura (R). Although considerable variation exists within island populations, these individuals typify the differences between the animals from the large, younger western islands on the main Sporades chain versus those from the older, eastern islands, which tend to have shorter legs and toes, bigger torsos, and a more dusky, gray-green coloration.

***Podarcis gaigeae*, Skyros wall lizard** (Werner, 1930)

The Skyros wall lizard is a narrow-range endemic species with a distribution centered on the Skyros island cluster, southeast of the focal area. In our study area, the species occurs only on the island of Piperi, which is inhabited by the endemic subspecies *P. g. weigandi* (see Gruber and Schultze-Westrum 1971). The individuals we observed on Piperi were normally sized for a *Podarcis* and did not exhibit gigantism of *P. gaigeae* populations from some Skyros satellite islets (Pafilis et al. 2009; Runemark et al. 2015). Thus, individuals from Piperi were similar in size to *P. e. ruthveni*, but had generally darker body coloration, often bright green backs, and dark dorsal reticulation. Gruber and Schultze-Westrum (1971) noted five criteria that distinguish *P. gaigeae* from *P. erhardii* in the Sporades: 1. Coloration: *P. gaigeae* has a strong green component to their dorsal coloration compared to *P. e. ruthveni*, which is more grey-brown to olive-brown. 2. Patterning: *P. gaigeae* has dark occipital spots, whereas *P. e. ruthveni* lacks occipital spots. 3. Femoral pores: *P. gaigeae* has more femoral pores, on average, compared to *P. e. ruthveni*. 4. Scalation: In *P. gaigeae*, the scutum masseteric abuts directly on the scuta supratemporalia more often than in *P. e. ruthveni*, and 5. Morphology: *P. gaigeae* has a relatively larger masseteric diameter than *P. e. ruthveni*.

Similar to other *Podarcis* species, *P. gaigeae* is a generalist that can be found in almost every habitat type. On Piperi, this species was most abundant in open areas near the settlement and at forest margins near the rocky coast, and less abundant in closed forested areas.

Snakes

The Sporades harbor eight snake species from three families: *Dolichophis caspius*, *Elaphe quatuorlineata*, *Hierophis gemonensis*, *Platyceps najadum*, *Telescopus fallax*, and *Zamenis situla* (all Colubridae), *Malpolon insignitus* (Psammophiidae), and *Vipera ammodytes* (Viperidae). We report here on nine new island records for: *D. caspius* (2), *E. quatuorlineata* (2), *T. fallax* (2), *V. ammodytes* (1), *Z. situla* (1), and *H. gemonensis* (1). We also observed a non-viperid snake species on the islet of Agios Georgios (between Skopelos and Alonnisos), but the species could not be identified.

***Dolichophis caspius*, Caspian whipsnake (Gmelin, 1789)**

We recorded the species for the first time on the island of Skatzoura (Fig. 4F) and the nearby islet of Prasso, which likely confirms the unspecified snake observation by Buchholz and Schultze-Westrum (1964) from there. Four large individuals were found on Skatzoura near stonewalls close to abandoned buildings, and an additional subadult was seen moving along the ground in the same area. We observed traces of rodents in and around these buildings, suggesting a good prey resource for this species. On the islet of Prasso, we found a large *D. caspius* basking in the sun, and later we collected a shed skin of the same species from elsewhere on the island. This species tends to be the only diurnal large-bodied colubrid on the islands where it is present. The Caspian whipsnake was previously recorded on the small islet of Lechousa, north of Peristera (Buchholz and Schultze-Westrum 1964), then on Alonnisos (Cattaneo 1998, 2010), and then Peristera itself (Kalogiannis 2021). The species has not been reported from Skiathos, Skopelos, Kyra Panagia, or Gioura, where *E. quatuorlineata* and/or another large colubrid species exist.

On the Sporades, the Caspian whipsnake reaches up to 160 cm in total length, thus approaching the largest lengths for its species known across Greece (the length-record being 208 cm from Samos; Cattaneo 2003). The species is common in the archipelago and is encountered in a diversity of habitats ranging from agricultural

land (wheat fields, olive groves, and vineyards) and areas near human habitation, to pine and juniper forests, as well as maquis and phrygana vegetation. Notably, it even occurs on relatively small islands like Lechousa and Prasso, where extensive exposed bedrock limits the amount of evergreen woody vegetation. The species feeds primarily on rodents but is opportunistic and will pursue birds, invertebrates, and reptiles, including other snakes (Speybroeck et al. 2016; Plettenberg-Laing and Mee 2020). On Alonnisos, we found individuals preying on lizards (e.g., *A. kitaibelii*, *L. trilineata*), snakes (*V. ammodytes* and other *D. caspius*), and large rodents, while Cattaneo (1998) also reports finding rabbit remains in ingesta content. Thus, it is a significant, generalist predator of a broad range of species, including its own, and a strong competitor with other snake species. Melanism is prominent among the populations of Alonnisos and Peristera, with several melanistic individuals encountered by the authors and others (Cattaneo 1998; Broggi 2010; Kalogiannis 2021).

Specimens: Skantzoura (NHMC 80.3.117.58).

Photographic voucher: Prasso (NHMC 80.3.117.70).

Elaphe quatuorlineata, four-lined rat snake (Lacépède, 1789)

We report here on two newly documented populations of this species on the island of Gioura (Fig. 4C) and the nearby islet of Grammeza. One adult male (SVL 126 cm; total length 155 cm) and a sub-adult male (SVL 71 cm; total length 89 cm) were found on Gioura, and another large adult male (SVL approximately 115 cm with a damaged tail) was found on Grammeza. In addition, we also report here an earlier, unpublished discovery of a subadult photographed near the Bay of Agios Petros on Kyra Panagia (Genevieve Leaper 2020 on iNaturalist).

Early publications had previously reported this species only from Skiathos (Buchholz and Schultze-Westrum 1964; Cattaneo 1997) and Skopelos (Buchholz and Schultze-Westrum 1964; Cattaneo 1998). We confirm the presence of the four-lined snake on Skiathos, where we found four juveniles and one sub-adult. We encountered *E. quatuorlineata* in a variety of habitats on Skiathos, such as olive groves, riparian forests, shrubland, and often near settlements, where it seems to be common. On the eastern islands, we found this species in rocky habitats with phrygana and maquis. This is the largest rat snake in Greece and can reach total lengths up to 200 cm on the mainland, though island populations usually tend to be smaller. On the Cyclades, the species reaches sexual maturity at substantially shorter total lengths (60–80 cm) (Speybroeck et al. 2016). For the Sporades, Cattaneo (1997, 1998) reported specimens with total lengths up to 180 cm on Skiathos and Skopelos. The four-lined snake primarily feeds on rodents and birds, though juveniles feed on lizards as well. On Grammeza, large adults likely also prey on rabbits that have been released and are now numerous on the islet. This was evident in the single adult we found, who exhibited several healed injuries throughout its body, a phenomenon usually attributed to theriophagy (Cattaneo 1998). All adult individuals from the Sporades exhibited the typical phenotype with four dark dorsal lines on a light, beige-yellow background (Fig. 4C). Juveniles from Skiathos showed the typical phenotype for their developmental stage, with dark blotches on a light background, similar to mainland populations, and a pink-red ventral area.

Photographic vouchers: Gioura (NHMC 80.3.31.37) and Grammeza (NHMC 80.3.31.38).

Hierophis gemonensis, Balkan whipsnake (Laurenti, 1768)

We confirm the presence of this species on the small island of Tsougria (Fig. 4J), near Skiathos. A juvenile individual was found in the rock ruins of a building in the vicinity of the coastal wetland area. This species was first recorded in the Sporades from Aspronisi (Buchholz and Schultze-Westrum 1964) and then from Tsougria (Grano et al. 2013), but has not been recorded from Skiathos itself. We also report on a previously unpublished record from Skopelos, confirmed by a specimen deposited in the Alexander Koenig Museum of Natural History in Bonn by T. Schuze-Westrum and W. Weigand on August 25th, 1957. However, we were not able to confirm this species during our own field work, neither on Skopelos nor on Aspronisi, perhaps due to inappropriate timing or low densities. Ultimately, *H. gemonensis* could be present on Skiathos, as the conditions seem suitable, and it is present on a nearby smaller island, though this remains speculative at present. The *H. gemonensis* documented in the Sporades does not exhibit markedly different phenotypes from the mainland populations.

Specimens: Tsougria (NHMC 80.3.25.134), Skopelos (ZMFK 003606)

Malpolon insignitus, Eastern Montpellier snake (Geoffroy Saint-Hillaire, 1827)

Eastern Montpellier snakes have a broad distribution in the lowlands of the Aegean-Anatolian region but do not survive well in island environments. In the Aegean archipelago, their distribution is restricted to the largest, young, near-shore landbridge islands. This conspicuous snake is common and well documented, both from Skiathos (Buchholz and Schultze-Westrum 1964; Cattaneo 1997) and Skopelos (Werner 1930, 1938a; Buresch and Zonkow 1934; Wettstein 1953; Mertens and Wermuth 1960; Buchholz and Schultze-Westrum 1964; Cattaneo 1998). We confirm this species on Skiathos (n=4), as well as Skopelos (n=20), but on no other islands, despite past speculation about its existence on Gioura and Skantzoura (Legakis 2004). Furthermore, a report of the species from Alonnisos (Crucitti and Tringali 1987; Legakis 2004) almost certainly refers to a misidentified *D. caspius* (Cattaneo 1998).

The Eastern Montpellier snake is a large-bodied species (record length in Greece is 160 cm; Kalogiannis and Stefanopoulos 2023) and a very active, diurnal hunter. We often encountered this snake in human-modified environments, including agricultural fields, olive groves, and near settlements, as well as in forested areas and maquis. It is a significant terrestrial predator with a catholic diet and a likely competitor to a number of other snake taxa. We found individuals preying on *P. erhardii*, while Cattaneo (1998) reports mammal and bird remains in stomach content, thus indicating that the species is largely euryphagous on the islands. Adults on Skopelos ranged from 80 cm to 140 cm in total length.

Platyceps najadum, Dahl's whipsnake (Eichwald, 1831)

This species is only documented in the Sporades on the island of Skiathos, where it is common (Bergman 1985, 1995; Cattaneo 1997). We found 13 individuals throughout the island and across a diversity of habitats, including agricultural land, settlements, mesic forested areas, and xeric sites such as phrygana and maquis. The largest individual had a total length of 125 cm. This is a very thin, quick, and agile snake that is also common on mainland Greece. It primarily feeds on small lizards and invertebrates (Speybroeck et al. 2016). Specimens from Skiathos exhibited the same typical phenotype as those from the nearby mainland, with about 25–30 ocelli across the front half of the body.

Telescopus fallax, cat-eyed snake (Fleischmann, 1831)

While this is a relatively widespread species on the Aegean islands, in the Sporades it has previously only been reported from Alonnisos (Broggi 2010). We report here for the first time two new photographic records from Peristera (Vasiliko bay area, August 2020; Vassilis Malamatenios) and the eastern part of Skopelos (August 2018; Luca di Cianni) (Appendix 1: Table A1). We also confirm the Broggi (2010) record (based on an unpublished photograph) with 12 individuals found in various locations around Alonnisos (Fig. 4G). This species is thinly distributed on Alonnisos and is more common at higher elevations in the central and eastern parts of the island, where the habitat is more xeric and rockier. Cat-eyed snakes are nocturnal, and we found most of them on Alonnisos while they were actively crossing roads or moving across rocky terrain at night (n=9), as well as under metal lids that cover concrete wells (n=3). This taxon is rear-fanged and venomous, though it is not considered a threat to humans as it rarely injects venom (Kochva 1965). The snake feeds mainly on geckos and lacertid lizards, which are abundant in the arid, sparsely vegetated areas this snake prefers.

Photographic voucher: Peristera (NHMC 80.3.38.147), Skopelos (NHMC 80.3.38.148).

Zamenis situla, leopard snake (Linnaeus, 1758)

We report here the presence of this species on Alonnisos, as supported by a photograph deposited in the NHMC (November 2020; Konstantina Malamateniou, see Appendix 1: Table A1). Thus, we confirm Broggi (2010), who mentions having seen pictures of the species taken by a local on Alonnisos but did not include them in his publication. We did not encounter any *Z. situla* during our field observations. The species has previously been recorded on Skiathos (Bergman 1995; Cattaneo 1997) and Skopelos multiple times, where both the striped and blotched phenotypes occur (Werner 1929, 1930, 1938a; Buresch and Zonkow 1934; Wettstein 1953; Buchholz and Schultz-Westrum 1964; Bruno 1969; Sigg 1984; Cattaneo 1998).

Zamenis situla is a colorful, slender, medium-sized snake that occurs in a blotched and striped form across its range (Speybroeck et al. 2016). On the Sporades, most individuals have red dorsal blotches outlined in black on a light-grey background with lateral spots. Additionally, there exists a striped form with a dorsal pattern of red stripes, or where the dorsal pattern is lacking any red and has more of a ladder-like black/dark gray bars. The species is typically more common near human habitations, giving it its Greek name, '*Spitofido*' (house snake). It appears to be uncommon on the Sporades.

Photographic voucher: Alonnisos (NHMC 80.3.30.82).

Vipera ammodytes, nose-horned viper (Linnaeus, 1758)

We report this viper for the first time from the island of Peristera (Fig. 4B). The specimen was a female about 40 cm in total length and had a light brown dorsal zig-zag band on a light beige background, resembling the phenotype of females from adjacent Alonnisos. The animal was found in one of the few open areas of the island, at the margins of a wet meadow and abandoned agricultural habitat invaded by patchy maquis.

This species had previously been recorded from Skiathos, Alonnisos, Megalos Adelphos, and Mikros Adelphos (Buchholz and Schultze-Westrum 1964; Cattaneo 1997, 1998). It is absent from all of the islands to the north-east of Alonnisos (e.g., Gioura, Legakis 2004). It also has not been documented yet in Skopelos, where the locals, however, claim it is present. On Skiathos, it is uncommon, and we did not observe any there during our surveys. Others have reported that individuals on Skiathos are relatively large (e.g., a male specimen of 53.2 cm reported by Buchholz and Schultze-Westrum 1964). Female *V. ammodytes* from Skiathos have the same phenotype as conspecifics from the adjacent mainland, with a dark brown dorsal zigzag pattern on a light brown background (Cattaneo 2021). In contrast, females from the islands of Alonnisos and Peristera exhibit a distinct phenotype that is very "washed out" or "blonde," which blends in well with the light-grey limestone bedrock of the island

(Fig. 4B and see fig. 8 in Cattaneo 2021). This female phenotype appears to be unique to Alonnisos and Peristera, according to extensive comparisons across numerous Aegean Sea islands (Roussos 2015; Cattaneo 2021). Males from Alonnisos have faint (or lack) lateral spots along the body, and the tail tip is black instead of green or yellow as found on the mainland. *Vipera* from Skiathos and Alonnisos also differ in scalation, with snakes from Skiathos possessing more dorsal scale rows (Cattaneo 2021). In contrast to Skiathos, the species is common on Alonnisos and can be found in a variety of habitats and at all elevations. A total of 25 observations have been made by the authors across the island near stone walls, settlements, phrygana, olive groves, maquis, and pine forest. Several individuals we found were victims of road mortality, especially during the mating period (May–June), as snakes tend to move during post-copulation dispersion. The largest individual we found on Alonnisos was a male with a total length of 75 cm, and others have recently reported individuals > 50 cm SVL (Cattaneo 2021).

Vipers are typically not able to survive on smaller islands. In the Sporades, the two small islands of Mikros and Megalos Adelphos are exceptional in that they retain viper populations. Vipers on the Adelphia cluster exhibit dwarfism (total adult lengths of 20–30 cm), similar to some Cycladic islands (e.g., Koufonissi, Roussos 2015; Itescu et al. 2018). The only size-appropriate prey items available on these islands are geckos and *Podarcis* lizards, *Scolopendra* centipedes, and, according to Buchholz and Schultze-Westrum (1964), Orthoptera, especially during the summer months. The islands are covered by a mixture of phrygana with some maquis bushes, as well as a few olive and juniper trees. Goats are also present and keep the shrubs heavily manicured. Vipers were found active during the day and near these bushes. The viper populations on these two small islands appear to be relatively dense, and this is the only snake species occurring there. While previous researchers (Buchholz and Schultze-Westrum 1964) have suggested that the vipers may prey on migratory birds, this is, in our opinion, unlikely, as the extremely small viper body size all but precludes the consumption of birds, except perhaps small songbirds by the largest individuals (>30 cm). What is more likely is that snakes benefit indirectly from the marine nutrient subsidies delivered by the strong gull colonies. Indeed, data from other islands in the Aegean Sea suggests that the presence of significant marine subsidies allows for the existence of predators on islands that would normally be considered too small to support them.

Photographic voucher: Peristera (NHMC 80.3.40.61).

Testudines

Only two Testudine species, each from a different family (Testudinidae and Geoemydidae), are present in the Sporades. We report here on one new island record for *Testudo marginata*. Testudines are the rarest group of native herpetofauna on these islands and appear to be continually declining. A variety of threats to their habitat make the long-term future of Testudines uncertain outside of protected areas (Hailey and Willemsen 2003).

***Testudo marginata*, marginated tortoise (Schoepff, 1789)**

The marginated tortoise is known from several islands in the Northern Sporades archipelago, where it has been documented on Skiathos (Cattaneo 1997), Alonnisos (Broggi 2010), and Kyra Panagia (Kock and Storch 1979). This species is also known from the neighboring Skyros cluster, including Skyros proper (Watson 1962; Arnold and Burton 1978; Kock and Storch 1979; Bringsoe 1985; Broggi 2006), and offshore Valaxa island (Gruber and Fuchs 1977). The marginated tortoise appears to be rare on the Sporades, with only occasional recorded encounters.

Here we document for the first time the presence of the marginated tortoise on Skopelos, therefore completing the known occurrence of the species across all major islands of the Sporades chain. On Skopelos, we encountered one adult male (carapace length 25 cm) crossing a dirt road in an agricultural area in the eastern part of the island. We also confirm the presence of *T. marginata* on Kyra Panagia, where we found two alive and two deceased adult specimens. All animals were encountered either in areas with maquis or near agricultural land. All four individuals found on Kyra Panagia were large, full-grown adults, and one of the live specimens had a healed injury to its carapace.

Photographic voucher: Skopelos (NHMC 80.3.22.18).

***Mauremys rivulata*, Balkan terrapin (Valenciennes, 1833)**

The Balkan terrapin has been reported from 31 Aegean and Ionian islands (Broggi 2023), where many of their populations have significantly declined over the last decades and, on some islands, are expected to go extinct (Broggi 2012). This species seems to only be doing well on larger islands with a substantial number of wetlands, such as on Evia (Euboea), Lesvos (Mytilene), Limnos, Ikaria, and Naxos (Broggi 2012; Strachinis and Roussos 2016). On the Sporades, the Balkan terrapin was first reported by Cattaneo (1997) from Skiathos, where small populations currently occur in the stream estuaries of Troulos and Agia Paraskevi. We observed 10 individuals in the streams of Troulos during the summer, where locals have put up signs to dissuade the taking of turtles. Here, the terrapins are regularly fed by tourists and are quite tame. This species is also very likely present in Vromolimnos marsh, but the dense vegetation has made observing them difficult. The Balkan terrapin is also present on Skopelos, where Cattaneo (1998) found a few specimens in the small pond of Ditropo. Furthermore, single individuals of this species have been observed in the coastal marsh of Milia (Broggi pers. comm.). Therefore, similarly to other regions of the Aegean Sea, terrapins in the Sporades survive only in a few isolated, relict wetland sites, and are likely threatened with extinction with the removal of these habitats (Cattaneo 1997; Broggi 2023).

Discussion

The herpetofauna of the Sporades archipelago has been investigated by herpetologists, both foreign and domestic, for almost a century, creating an intriguing but incomplete picture of the biodiversity in this region (Werner 1930; Cyrén 1935). Our 7+ year survey documents 26 new island records of lizards, snakes, and tortoises, confirms 5 unvalidated lizard and snake records, and finds 3 records in the literature erroneous. This is the first review and most comprehensive species account of the Sporades herpetofauna to date.

Biogeography of the islands: Patterns of island diversity and underlying processes

Despite the relatively small extent of the Sporades archipelago, the islands vary significantly in species richness and herptile community structure (Figs 2, 3, Tables 1, 2). At the most basic level, the species assemblages of the Sporades are derivative of those from the Thessaly mainland. Island species richness declines with decreasing island size but also with increasing island age (age of insularity), with the oldest islands in the east having much more depauperate herptile species communities relative to the younger, larger islands in the west (Fig. 2). Thus, Lechousa, a small, young island with a recent landbridge connection to Alonnisos and the Thessallian mainland, has as many herptile species (3) as the almost 20× larger Gioura located off the mainland shelf. Given that the landbridge islands most likely shared the same species assemblages during the last ice age when they were connected (Foufopoulos et al. 2011), present-day differences in species richness are best interpreted as the outcome of differential extinctions.

Recent research has shown that Holocene reptile extinctions in the Aegean are highly predictable and are determined by both species identity and island characteristics (Kalb 2021). Thus, larger-bodied species (e.g., lizards like *P. apodus* or snakes like *M. insignitus*), as well as habitat specialists (such as the moisture-loving species *L. trilineata* and *M. rivulata*), tend to have smaller populations and are more likely to go extinct first following isolation by rising sea levels (Foufopoulos and Ives 1999). Because the particular species' life history traits determining extinction sensitivity are the same across an archipelago, species tend to go extinct in a predictable sequence across all islands, reflecting each taxon's relative susceptibility to underlying extinction drivers. What varies is the extent to which island characteristics cause the original species community to progress down the general sequence of species loss. Thus, islands that are smaller, older, more rugged, and have less water, (e.g., Skantzoura, Piperi, and Gioura) tend to lose a higher fraction

Table 1. Distribution of reptiles across the study islands of the Sporades, together with supporting sources. The table contains the bigger islands in an approximate west-to-east direction. Bolded text indicates records newly reported in this paper.

Species	Skiathos	Skopelos	Alonnisos	Peristera	Skantzoura	Kyra Panagia	Gioura	Piperi
M. rivulata	+ 2, 16, 17	+ 3						
T. marginata	+ 2*	**+ 1**	+ 15			+ 7		
M. kotschyi		+ 8	+ 3, 8	+ 8	+ 8	+ 8, 17	+ 8	**+ 1**
H. turcicus	+ 2	+ 9	+ 3, 10	**+ 1**		**+ 1**		+ 12
P. apodus	+ 13	+ 25						
L. t. trilineata	+ 3, 11	+ 3, 11	+ 3, 10, 14, 15					
P. erhardii	+ 13	+ 3, 14, 20	+ 3, 10, 14	+ 18	+ 18	+ 18	+ 14	+ 10 (*P. gaigeae weigandi*)
A. kitaibelii	+ 2	+ 3, 14	+ 3, 10, 15					
D. caspius			+ 3, 4	+ 5	**+ 1**			
H. gemonensis		+ 26						
P. najadum	+ 2, 13							
E. quatuorlineata	+ 19	+ 3, 19				+ 6, 25	**+ 1**	
Z. situla	+ 2, 13	+ 3, 16, 17, 19	+ 15, 25					
M. insignitus	+ 2, 13, 19	+ 3, 16, 19						
T. fallax		+ 25	+ 15	+ 25				
V. ammodytes	+ 2, 19		+ 3	**+ 1**				
P. kurtmuelleri	+ 2	+ 3, 14	+ 10, 15**					
B. viridis		+ 3, 14						
H. arborea	+ 2							

1 – New record by authors; 10 – Grillitsch and Tiedemann (1984); 19 – Buchholz and Schultze-Westrum (1964)
2 – Cattaneo (1997); 11 – Sagonas (2019); 20 – Wettstein (1957a)
3 – Cattaneo (1998); 12 – Daftsios et al. (2024) ; 21 – Crucitti and Tringali (1987)
4 – Cattaneo (2010); 13 – Bergman (1995); 22 – Grano et al. (2013)
5 – Kalogiannis (2021); 14 – Cyren (1935); 23 – Froer (1979)
6 – Legakis et al. (2004); 15 – Broggi (2010); 24 – Chondropoulos (1986)
7 – Kock and Storch (1979); 16 – Werner (1930); 25 – Record by citizen photographers or from iNaturalist (Appendix Table A1).
8 – Beutler and Gruber (1977); 17 – Werner (1938a); 26 - Alexander Koenig Museum of Natural History in Bonn
9 – Gruber (1974); 18 – Gruber and Schultze-Westrum (1971);
*Cattaneo (1997) identifies this individual as *T. hermanii*, it was likely a misidentified juvenile *T. marginata*
***P. kurtmuelleri* is considered likely extinct on Alonnisos, see species accounts section

Table 2. Distribution of reptiles across the study islands of the Sporades, together with supporting sources. The table contains the smaller islands in an approximate west-to-east direction. See Table 1 for supporting sources.

Island Code	Island Cluster	Island Name	*Mediodactylus*	*Podarcis*	*Hemidactylus*	*Lacerta*	Other
TSA	Skiath	Tsougria			+ 22	+ 22	+ *H. gemonensis* – 22
TSI	Skiath	Tsougriaki	+ **1**	+ 18			
ARK	Skiath	Arkos	+ **1**	+ 18	+ **1**	+ 17, 23, 24	
MAR	Skiath	Maragos		+ 18			
ASP	Skiath	Aspronisi		+ 18			+ *H. gemonensis* – 19
REP	Skiath	Repi	+ 8	+ 18			
DAK	Skiath	Daskalonisi	+ **1**				
PAX	Skop	Paximadi (Skop)	+ **1**				
STR	Skop	Strongyllo (Skop)		+ 26			
DAS	Skop	Dasia (Skop)		+ 18			
KAS	Skop	Kassidis (Skop)	+ 8				
PLE	Skop	Plevro (Skop)		+ 18			
AGG	Skop	Agios Georgios	+ **1**	+ 18			Snake confirmed***
MIK	Skop	Mikronisi	+ **1**	+ 18			
KOK	Alon	Kokkinokastro		+ 18			
MAN	Alon	Manolas	+ 26	+ 18			
LEO	Alon	Lechousa	+ 8	+ 18			+ *D. caspius* - 19
MEA	Alon	Megalos Adelphos	+ 8	+ 18			+ *V. ammodytes* – 19
MIA	Alon	Mikros Adelphos	+ 8	+ 18			+ *V. ammodytes* – 19
GAI	Alon	Gaidaronisi	+ 8	+ 18			
POL	Skantz	Polemika	+ **1**	+ 18			
LAC	Skantz	Lachanou		+ 18			
KSD	Skantz	Kassidis		+ 18			
KYR	Skantz	Kyriagos	+ **1**	+ 18			
PRA	Skantz	Prasso	+ **1**	+ 18			**+ *D. caspius* - 1**
SKA	Skantz	Skandili	+ **1**	+ 18			
MKS	Skantz	Mikroskandili		+ 18			
KOR	Skantz	Korakas	+ **1**	+ 18			
AGP	KyrPan	Agios Petros		+ 17, 18			
PEL	KyrPan	Pelerissa	+ **1**	+ 18			
MEL	KyrPan	Melissa	+ 8	+ 18			
SFI	KyrPan	Sfika		+ 18			
PAP	KyrPan	Pappous		+ 18	+ 9, 24		+ *H. turcicus* – 9
KOU	KyrPan	Koumbi	+ 8	+ 18			
GRA	KyrPan	Grammeza	+ 8	+ 18			**+ *E. quatuorlineata* – 1**
MYG	Gioura	Myga		+ 18			
PSA	Gioura	Psathoura	+ 14,8	+ 18			

*** Observation of a snake confirmed, possibly *D. caspius*, *H. gemonensis*, or *M. insignitus*.

of their original species communities (Kalb 2021). Ultimately, this results in a distinct pattern of nested species occurrences where smaller and older islands support only species found on larger ones. The only exception to this pattern is species that likely inhabit similar ecological niches, such as *E. quatuorlineata* and *D. caspius*, which do not co-occur on the same island in the Sporades (though we note these species do co-occur in the Cyclades islands), but instead show characteristic ‘checkerboard’ distributions (Diamond 1975). Furthermore, some species, such as *Mediodactylus* and *Podarcis*, display a phenomenon called density compensation, occurring in more dense populations and having broader habitat utilization on smaller, species-poor islands relative to large islands (Rodda and Dean-Bradley 2002). This means that they are sometimes rare and very hard to detect on larger islands, such as *Mediodactylus* on the larger Sporades.

Skiathos is the island closest to the species-rich Thessaly mainland and was last connected to it until fairly recently (~8.5 kya). Because extinction, which is a time-dependent process, has had less time to act on the resident species communities, the island retains a greater fraction of the original mainland species communities, being the Sporades island with the most snake species and the only island that retains both *P. najadum* and *H. arborea*. Skiathos has more significant wetland areas compared to other larger islands to the east, with 1% of its total surface covered by freshwater (Catsadorakis and Paragamian 2007). Interestingly, *M. kotschyi*, one of the most widely distributed species in the archipelago, has not yet been recorded from the island, even though it occurs on the surrounding satellite islets (Tsougkriaki, Arkos, and Daskalonisi). Similarly, *H. gemonensis* has been recorded from two islets off Skiathos (Tsougria and Aspronisi) but not yet from Skiathos itself.

The island pair of Skopelos and Alonnisos have been isolated almost twice as long as Skiathos from the mainland (15 kya, see Fig. 1, 3) yet harbor similar numbers

of taxa. Because Skopelos is more densely forested and retains more wetland areas than Alonnisos, it still sustains several hydrophilic species (*P. kurtmuelleri*, *B. viridis*, and *M. rivulata*), the latter of which is likely lost to extinction. Snake communities between the two islands also differ somewhat, with only Skopelos harboring *M. insignitus*, *H. gemonensis*, and *E. quatuorlineata*, while Alonnisos harbors *V. ammodytes* and *D. caspius* instead. This pattern is likely caused by a combination of inter-island differences in habitat in conjunction with interspecific competition between the various snake species.

Skantzoura, Kyra Panagia, and Gioura have all been isolated for longer periods of time, are smaller by land area, and have lower habitat diversity than the main three islands to the west. These smaller islands and their satellite islets are surrounded by very deep waters (> 120 m), suggesting a very long period of isolation (> 200 kya and possibly up to 5.3 million years coinciding with the Zanclean flood; Rohling et al. 2014, assuming depths have not changed significantly due to tectonic movement).

Relatively few exotic reptile introductions appear to have occurred to date on the Sporades, and most species appear to be native to the islands. Three possible exceptions to this are the tortoise *T. marginata*, the gecko *H. turcicus*, and the skink *C. ocellatus* (assuming the Skopelos record is not erroneous). The former is often kept as a pet (Valakos et al. 2008) and may have been introduced in this manner onto the larger, human-inhabited islands of the archipelago. The latter two lizards are often transported by virtue of their small body size, peri-domestic occurrence, and their tendency to hide in building materials and livestock feed. Genetic analyses indicate that for both species, lizard populations across the Mediterranean lack genetic structure, consistent with recent anthropogenic transportation (Kornilios et al. 2010; Rato et al. 2011; Ergül Kalayci et al. 2023). In accordance, we encountered *H. turcicus* only on islands regularly visited by humans.

Reptile and amphibian habitat use in the Sporades

While reptiles occupy most natural habitats in the Sporades, some habitats are clearly more important than others and require particular management attention (see Table 3). In general, both amphibian and reptile taxa prefer wetter and more productive habitats, especially if they provide enough insolation for thermoregulation. Wetland areas are the most important habitats because, at least during the summer season, they serve as oases, allowing species to persist in an otherwise hostile habitat.

While conservation emphasis often centers on the actual water bodies, the surrounding habitats can be equally important. We found that the wet meadows surrounding many coastal wetlands were not only used by most of the local reptile and amphibian species, but that they were, when not degraded, extremely species-rich for many other organisms, including plants and invertebrates. We identified such wet meadows in Koukounaries, Aselinos, and Platanias (Skiathos), but also in Tsougria, in Livadakia (Peristera), and in Agios Petros (Kyra Panagia). Wet meadows face immense pressure not only from touristic development but also from overgrazing and undergrazing, which can result in the encroachment of shrubs and exotic invasives.

On the other hand, extensively shaded areas like pine forests are avoided by most taxa, presumably because they lack opportunities for thermoregulation. Our field observations also suggest that structurally and thermally diverse habitats, such as traditional agricultural landscapes, are disproportionately significant because they provide abundant thermoregulatory opportunities for resident species (Zakkak et al. 2015). For example, dry stone wall terraces, a common feature of agriculture fields on sloped island landscapes, not only create a varied set of thermal environments, but also offer valuable refugia from predation since they are challenging for snakes to ascend (Nossan 2023). Overall, most species of reptiles on the Sporades, with the exception of aquatic taxa, appear to be behaviorally quite flexible and can be found in numerous native and human-modified habitats.

Anthropogenic changes in the landscape of the archipelago

Over the last century, human communities on the Sporades have experienced significant demographic and economic shifts with important ramifications for the ecology and herpetofauna of the islands. Extensive agricultural areas were abandoned, first because of a lack of economic incentives and emigration to urban centers, and again more recently with the emergence of tourism as a more lucrative income alternative. As a result of these changes, all of the smaller island settlements were completely abandoned in the last 50 years (Tsougria, Megalos Adelphos, Skantzoura, Grammeza, Pappous, Gioura, Psathoura, and Piperi) (Wikipedia n.d., National Statistical Service of Greece 2011). On the larger islands, and over the last 80 years, abandonment of traditional agricultural activities has progressively led to the incursion of tall maquis and pine forests. Vegetation modulates microclimates (Osorio et al. 2024), and changes to land cover seriously alter thermal landscapes that ectotherms like herpetofauna use to behaviorally maintain homeostasis. In general, shifts to a more closed vegetation structure are associated with a narrower, cooler thermal gradient that results in a greater mismatch to body temperatures preferred by herpetofauna and therefore decreased thermoregulatory efficiency (Muñoz and Losos 2018). Thus, the widespread shift to closed-canopy pine forest in the Sporades has likely decreased opportunities for efficient herptile thermoregulation, as evidenced by their general dearth in such habitats (Table 3).

Table 3. Habitat use of reptiles and amphibians on the Sporades as determined by our observations.

Species	Abbrev	Settlements	Grain fields	Streams/ wetlands	Gardens/ vineyards	Olives	Phrygana	Pine forest	Maquis	Rocks	Habitats Used
Mauremys rivulata	MR	0	0	1	0	0	0	0	0	0	**1**
Testudo marginata	TM	0	0	0	1	1	1	0	1	0	**4**
Mediodactylus kotschyi	MK	0	1	0	1	1	1	1	1	1	**7**
Hemidactylus turcicus	HT	1	1	1	1	1	1	1	1	1	**9**
Pseudopus apodus	PA	0	0	1	1	1	1	0	1	1	**6**
Lacerta trilineata	LT	1	0	1	1	1	1	1	1	1	**8**
Podarcis erhardii	PE	1	1	1	1	1	1	1	1	1	**9**
Podarcis gaigeae	PG	1	1	1	1	1	1	1	1	1	**9**
Ablepharus kitaibelii	AK	1	1	1	1	1	1	1	1	0	**8**
Dolichophis caspius	DC	1	1	1	1	1	1	1	1	1	**9**
Hierophis gemonensis	HG	0	0	1	1	1	1	0	1	1	**6**
Platyceps najadum	PN	0	0	1	1	1	1	1	1	1	**7**
Elaphe quatuorlineata	EQ	1	1	1	1	1	1	1	1	1	**9**
Zamenis situla	ZS	1	1	1	1	1	0	0	1	1	**7**
Malpolon insignitus	MI	1	0	1	1	1	1	1	1	1	**8**
Telescopus fallax	TF	0	0	0	1	1	1	0	1	1	**5**
Vipera ammodytes	VA	1	0	0	1	1	1	1	1	1	**7**
Pelophylax kurtmuelleri	PK	0	0	1	0	0	0	0	0	0	**1**
Bufotes viridis	BV	0	0	1	0	1	0	0	0	0	**2**
Hyla arborea	HA	1	0	1	1	0	0	0	0	0	**3**
Total Species		**10**	**8**	**16**	**17**	**17**	**15**	**11**	**16**	**12**	

Livestock husbandry and reptiles

Livestock husbandry and the associated vegetation changes appear to have a complex relationship with the resident herpetofauna. In the relatively humid Sporades climate, browsing by goats is an important process for keeping vegetation open and preventing the establishment of a closed canopy. Research in other parts of the Aegean Sea region has demonstrated that the impacts on vegetation cover rise with an increasing stocking rate (Cheng 2015). In the Sporades, similar to other parts of the region (Gizicki et al. 2018), island size determines both the type of livestock husbandry, as well as the ultimate impacts on vegetation structure and the resident reptile community. On the larger islands with permanent human populations, individual families have traditionally kept small numbers of goats and sheep for personal use. In addition, a limited number of larger flocks of livestock were typically kept by shepherds who carefully managed grazing patterns to avoid crop damage. In these open and carefully managed agropastoral systems, our personal observations indicate a particularly high reptile presence. Thus, on the main islands, most species of reptiles prefer habitats moderately disturbed by grazing, and avoid (with the apparent exceptions of *D. caspius* and *A. kitaibelii*) undisturbed, closed-canopy pine forests. Even on medium-sized islands like Peristera and Skantzoura, reptiles are concentrated in open field areas maintained by goats and appear to avoid the expanding dense maquis.

In contrast to the controlled animal husbandry of large islands, on small islands and islets, goats are typically released unguarded for extended periods of time and left to forage freely. Given the limited resources there, goat releases on islets typically result in severe soil erosion and large-scale vegetation degradation (Gizicki et al. 2018). A formal study from the nearby Skyros cluster demonstrated that goat grazing on small islands has serious negative impacts on both plant cover and the resident herpetofauna (Pafilis et al. 2013). Our own field observations confirm that on islets smaller than a few hectares, livestock grazing results in negative outcomes for local species communities. Based on our field observations, many, if not most, of the smaller islands in the Sporades appear to have suffered from past overgrazing, which has shifted plant communities and severely damaged the vegetation cover. Pelerissa Isl., near Kyra Panagia, still bears the scars of past overgrazing, with the evident trunks of many kermes oaks killed by goats, and the ground covered by a degraded graminoid monoculture that is inhabited only by *Mediodactylus* and *Podarcis* (Fig. 6A).

While this practice has nowadays been largely discontinued on the smallest islets, several of the somewhat bigger, yet uninhabited islands (Gioura, Piperi, Grammeza, Peristera, Lechousa, Skantzoura, Megalos Adelphos, Mikros Adelphos, and Agios Georgios) still harbor populations of goats in different stages of abandonment and only thin *Podarcis* and *Mediodactylus* populations. Other islands (Repi, Grammeza) suffer similarly, but from released rabbits that dig out top soil, creating another form of erosion detrimental to the sustainability of vegetation (Kossoff 2023).

Habitat use and status of hydrophilic herpetofauna

Wetland ecosystems, both in the Aegean generally and on the Sporades specifically, are typically scarce, vulnerable, and disproportionately important for reptiles and

amphibians (Catsadorakis and Paragamian 2007). From the whole archipelago, Skiathos has the most notable wetlands and streams, which are nonetheless few and under human pressure. The marsh of Vromolimnos on Skiathos is in good condition, although some hotels and beach bars exist nearby. The wetland of Koukounaries, although modified, is also in relatively good condition and is now strictly protected, despite the presence of hotels constructed in the surrounding area before the lake's declaration as a nature reserve. The area of Koukounaries, including the lake, coastline, and *Pinus pinea* forest, is currently a Natura 2000 site (GR1430003). Skopelos possesses only three wetlands of significance, two of which are seasonal. The permanent lagoon of Milia is in seemingly good condition and hosts populations of frogs and terrapins. On Alonnisos, there is a single seasonal, coastal lagoon located at Agios Dimitrios. Additional small, typically seasonal wetlands exist on Tsougria, Peristera, Kyra Panagia, and Psathoura. Unfortunately, some of the natural wetlands of the archipelago have been reduced or completely destroyed by human activities during the last decades. On Skiathos, Skopelos, and Alonnisos, many wetlands, lagoons, and streams have been drained and built over for touristic development (e.g., hotels and airport infrastructure) or are heavily exploited for irrigation.

From the sites mentioned above, only the wetlands of Skiathos and Skopelos currently host hydrophilic reptiles and amphibians (*M. rivulata*, *B. viridis*, *P. kurtmuelleri*, and *H. arborea*). Green toads, *B. viridis* (Laurenti, 1768), are widespread throughout insular Greece, often inhabiting surprisingly small islets (e.g., Stille and Stille 2015; Strachinis 2022), where they commonly reproduce in artificial water bodies. Despite this, they can be severely affected by human activities and are known to have had significant population declines on some islands (e.g., Ithaki, Strachinis and Artavanis 2017). Similarly, marsh frogs of the genus *Pelophylax* are also well distributed across insular Greece (Valakos et al. 2008), occupying streams, marshes, lagoons, and artificial water bodies such as reservoirs and wells, where they greatly depend on these open water resources (Broggi 2021). In the Sporades, marsh frogs have vanished from Alonnisos, where, according to the locals, they used to thrive until the 1980's. Specific changes in irrigation, along with heavy exploitation and destruction of streams, caused frogs on Alonnisos to steadily decline, eventually dying out during the 2000's. Tree-frogs in the genus *Hyla* are less widespread in the Greek islands, occurring on Thassos, Skiathos, Evia, Corfu, Lefkada, Kefalonia, Zakynthos, Lesvos, Chios, Samos, Kos, Rhodes, and Crete (Valakos et al. 2008), islands known to have high freshwater availability (Catsadorakis and Paragamian 2007). On Skiathos, they seem to occur in abundance around settlements where they breed in anthropogenic structures such as swimming pools. Although they exist in seemingly good populations on the island, the aforementioned breeding sites are unreliable in the long term and readily impacted even by small changes in human activity. For the Balkan terrapins, both in the Sporades and in the rest of the Aegean, the main threats concerning the viability of island populations are habitat destruction and, in the long term, climate change (Broggi 2012). The populations of *M. rivulata* on Skopelos have significantly declined and have been limited to isolated waterbodies that are particularly susceptible to human activities and climate change.

Overall, habitat loss constitutes the main risk to amphibian and terrapin populations on the islands, since the remaining wetland habitats are now in small and isolated, relict sites. In addition to natural habitats, artificial water bodies (e.g., wells and canals) used for agriculture serve as important breeding sites for green toads and marsh frogs on Aegean islands. Nonetheless, these breeding sites are disappearing as traditional cisterns are being replaced by the modern irrigation system. Consequently, the conservation of wetland habitats, as well as of traditional agriculture, is crucial for the survival of amphibians and terrapins in the Sporades archipelago.

Management and conservation recommendations

The maintenance of healthy reptile and amphibian communities is directly tied to appropriate habitat management. On the western, more developed islands, the main threats to the native communities are road construction, touristic development, and surface water diversion. On the smaller, eastern islands, the main problems center on the abandonment of the traditional agricultural activities, as well as the overgrazing of small islets. As a result, management recommendations differ among the islands. Given that many of the eastern islands are within the MPA and least threatened by human development, the terrestrial aspect of the reserve could be one of promising restoration and management. This would not only promote suitable habitat for the herptile community but also for all biota native to these islands. Another significant threat to reptile populations on human-inhabited Aegean islands are feral cats (Case and Bolger 1911). While spaying and neutering cats can help control their population numbers, it will not stop their killing of birds, small mammals, and reptiles. Outdoor cats are significant predators of snakes and lizards and have caused island extinctions the world over (Medina et al. 2011). We recommend that cats be kept indoors for their own health and safety and the preservation of biodiversity. Fortunately, smaller islands that do not have cats are refuges for snakes and lizards from this invasive predator.

Recommendations for large, human-inhabited islands

Our field research suggests that the continuation of traditional agricultural activities, including some goat grazing, which create a mosaic of thermally variable

microhabitats, is important for the persistence of native reptiles and amphibians (Papanastasis et al. 2009). This includes the preservation of the diverse stone structures such as drystone walls and terraces, stables, and cisterns, all of which provide cover and refugia for resident reptiles. In addition, maintenance of any sources of surface water, whether in the form of springs, seasonal streams, or cisterns, is essential for many species. The practice of illegally drawing water from springs and streams with small pumps for irrigation desiccates the landscape and is particularly damaging, and its prohibition should be enforced. On Skopelos and Skiathos, exurban development for tourism and associated roads is increasingly leading to the fragmentation of the natural habitats and represents a growing problem for native reptiles and amphibians.

Wetlands and wet meadows harbor many unique species and require urgent priority protection and management. On Skiathos and Skopelos, perhaps small ponds could be constructed in order to enhance the reproductive success of amphibian species. Wet meadows, such as the wetlands of Koukounaries and the mouths of the Aselinos stream (Skiathos), are tremendously important and require special management. This requires the absence of water extraction to maintain high water tables, the absence of plowing, and the removal of encroaching bushes, ideally through activities such as scything. Grazing, if it occurs, must happen only briefly, perhaps late in the summer, with a focus on controlling encroaching bushes.

We observed significant seasonal road mortality in certain areas, suggesting that the creation of under road tunnels would be an excellent way to allow for safer passages. These can be used as general wildlife crossings for other species as well. Road signage is a cost-efficient and educational strategy to warn drivers to slow down and be alert to species' crossings.

Recommendations for medium-sized, uninhabited islands

Overgrazing by unmanaged, feral goats constitutes the biggest problem for the resident herpetofauna on medium-sized, uninhabited islands. Overstocking on such islands can lead to dramatic habitat degradation through vegetation loss and subsequent soil erosion, as seen on Kyra Panagia and Pelerissa islands (Fig. 6A). Nonetheless, lower levels of grazing on some larger uninhabited islands can open up forest and dense maquis thickets and provide basking opportunities for local reptiles. On some islands where grazing pressure has declined significantly in the last few years (esp. on Peristera and Skantzoura), habitat quality for resident reptiles may be declining, as has been the case in other parts of Greece (Zakak et al. 2015).

Some of the medium-sized islands of the archipelago also include key wet meadows that exist today in severely overgrazed and degraded form: Livadakia (on Peristera) and Agios Petros (on Kyra Panagia). Given the importance of these habitats for reptiles, it would be important to eliminate grazing and plowing on these specific sites, something that on Agios Petros is particularly easy given that the property is already fenced in. In the medium term, additional restoration measures may be needed, including the re-introduction of some sensitive plant species as well as potential scything to prevent invasion of the bushes.

Recommendations for very small, seabird islets

While small islets harbor only a few reptiles and no amphibians, they are often disproportionately important for conservation because they tend to be free of human interference, act as important stop-over points for migrating birds, and often showcase unusual reptile populations with often extreme phenotypes. Lizards from seabird islands occur in extremely high population densities, possess unusually large body sizes, and often display exceptional territorial, cannibalism, or fearlessness behaviors (Brock et al. 2014, 2015; Donihue et al. 2016). Islet species communities are primarily dependent on the existence of large seabird colonies to provide marine nutrient subsidies (Stadler et al. 2023) and tend to be severely impacted by invasive goats, rabbits, and rats (Weber 2014; Gizicki et al. 2018). As a result, the removal of invasive species and the promotion of seabird colonies are the most important management activities for small island reptile populations .

Conclusion

Based on our surveys, we find that the herpetofauna of the Sporades is rich, and contains relatively few exotic taxa. Species communities are a subset of the neighboring mainland, and decline as mostly nested subsets with decreasing island size and increasing age of isolation, especially for the off-the -shelf islands. Endemic elements include the unique subspecies *Podarcis erhardii ruthveni* and *Mediodactylus kotschyi fuchsi*, with wide distributions across most of the archipelago. While none of the local non-aquatic populations appear outright endangered, many populations face pressures stemming primarily from habitat conversion and degradation. These occur under the combined effects of touristic development, including wetland destruction and abandonment of traditional agricultural activities. However, most species associated with wetlands and humid ecosystems (terrapins, amphibians) are in decline and require urgent protection of their habitats. By extension, wetlands and wet meadows harbor many unique species and require priority protection and management. Both overgrazing and undergrazing represent problems for the resident reptiles and amphibians, the former on small desert islets, and the latter on the larger, wetter islands.

Figure 6. Some of the habitats important for reptiles and amphibians across the Sporades. **A.** Impacts of overgrazing and habitat recovery on Pelerissa. Note the remnants of Kermes oak trunks killed by goats in the center and the expanding margins of recovered *Pistacia* bushes on the left; **B.** *Q. coccifera* forest and open area on the slopes of Gioura; **C.** Dry stone walls on one of the last open fields on Peristera; **D.** Recovering maquis vegetation on Grammeza, with Gioura in the background; **E.** Wetland on Tsougria; **F.** Expanding *Juniperus* forest on Skantzoura; **G.** Stream estuary on Skiathos; **H.** Human-created species-rich wet meadow on Skiathos.

Acknowledgements

This work has benefited from the support and contributions of numerous individuals. Dr. Petros Lymberakis (Natural History Museum of Crete) provided insight and logistical support in regard to collection permits and museum specimens. We are also greatly indebted to the Thalassa NGO, whose crew (Antonis Voutsinos, Josephina Zoulias, and Efi Miskedaki) selflessly transported us on their boat NIRIIS to many of the study areas. Special thanks also go to Valia Stefanoudaki (director of Sea Shepherd Greece) and the crew of MV Emannuel Bronner for helping with further transportation to the uninhabited islands. We also thank MoM NGO and, in particular, Panos Dendrinos for advice and on-the-ground assistance. We would also like to acknowledge the support of the management body of Alonnisos Marine Park, especially Spyros Iosifidis and Theodoros Mouratidis, for their tireless support. This work also benefited from the input of the Hellenic Society for the Study and Protection of the Monk Seal (MOm). This work was conducted under permits from the Greek Government (Ω6ΛΝ4653Π8-ΤΨΑ, ΔΔΔ/41002/1289, ΔΔΔ/26742/981, ΔΔΔ/29761/985).

References

Arnold E, Burton J (1978) A field guide to the reptiles and amphibians of Britain and Europe. Collins, London, 272 pp.

Băncilă RI, Lattuada M, Sillero N (2023) Distribution of amphibians and reptiles in agricultural landscape across Europe. Landscape Ecology 38(3): 861–874. https://doi.org/10.1007/s10980-022-01583-w

Barouda A, Quinn P, Efstratiou N (2023) Agios Petros and the Neolithic pottery-making traditions of the deserted islands, Northern Sporades, Greece. Archaeological and Anthropological Sciences 15(2): 16. https://doi.org/10.1007/s12520-022-01713-0

Bergman J (1995) Neues zur Herpetofauna der Insel Skiathos, Nördliche Sporaden, Griechenland. Herpetofauna 17(98): 26–28.

Beutler A, Gruber U (1977) Intraspezifische Untersuchungen an *Cyrtodactylus kotschyi* (Steindachner 1870); Reptilia: Gekkonidae. Beitrag zu einer mathematischen Definition des Begriffs Unterart. Spixiana, München l(2): 165–202.

Beutler A (1981) *Cyrtodactylus kotschyi* (Steindachner, 1870)—Ägäischer Bogenfingergecko. Handbuch der Reptilien und Amphibien Europas 1(1): 53–74.

Bintanja R, van de Wal R, Oerlemans J (2005) Modeled atmospheric temperatures and global sea levels over the past million years. Nature Letters 437: 125–128. https://doi.org/10.1038/nature03975

Bringsøe H (1985) A check-list of Peloponnesian amphibians and reptiles, including new records from Greece. Annales Musei Goulandris, Kifissia 7: 271–318.

Brock KM, Donihue C, Pafilis P (2014) New records of frugivory and ovophagy in *Podarcis* lizards from East Mediterranean Islands. North-western Journal of Zoology 10: 223–225.

Brock KM, Bednekoff PA, Pafilis P, Foufopoulos J (2015) Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? Evolution 69(1): 216–231. https://doi.org/10.1111/evo.12555

Brock KM, Baeckens S, Donihue CM, Martín J, Pafilis P, Edwards DL (2020) Trait differences among discrete morphs of a color polymorphic lizard, Podarcis erhardii. PeerJ 8: e10284. https://doi.org/10.7717/peerj.10284

Broggi MF (2006) Feuchtgebiete auf Skyros (Nördliche Sporaden-Griechenland) – ihre Beschreibung und einige ornithologische und herpetologische Inselbeobachtungen. Berichte Botanisch-Zoologische Gesellschaft Liechtenstein-Sargans-Werdenberg 31: 269–274.

Broggi MF (2010) The herpetofauna of Alonissos (Northern Sporades, Greece). Herpetozoa 23(1/2): 71–78.

Broggi MF (2012) The Balkan Terrapin (*Mauremys rivulata* (VALENCIENNES, 1833) in the Aegean islands. Threats, conservation aspects and the situation on the island of Kea (Cyclades) as a case study. Herpetozoa 24(3/4): 149–164.

Broggi MF (2021) The decline of the herpetofauna populations related to open water resources on Aegean islands using the example of Kythnos. Biodiversity Journal 12(4): 825–831. https://doi.org/10.31396/Biodiv.Jour.2021.12.4.825.831

Broggi MF (2023) Occurrence and tentative population status of the Balkan Terrapin (*Mauremys rivulata*, Valenciennes, 1833) on Greek islands. Herpetozoa 36: 233–247. https://doi.org/10.3897/herpetozoa.36.e100533

Bruno S (1969) Morfologia, distribuzione e biologia di *Elaphe situla* (Linnaeus) 1758. Atti della Accademia Gioenia di Scienza naturali in Catania 7(1): 1–44.

Buchholz KF, Schultze-Westrum T (1964) Zur Kenntnis der Schlangenfauna der Nördlichen Sporaden. Zoologischer Anzeiger 173(2): 127–136.

Buresch I, Zonkow J (1934) Untersuchungen über die Verbreitung der Reptilien und Amphibien in Bulgarien und auf der Balkanhalbinsel. Teil II: Schlangen. Mitteilungen aus den Königlich Naturwissenschaftlichen Instituten in Sofia 7: 106–188.

Buttle D (1995) Reptiles and Amphibians of the Greek Islands. Reptilian 3(7): 15–27.

Case TJ, Bolger DT (1991) The role of introduced species in shaping the distribution and abundance of island reptiles. Evolutionary Ecology 5: 272–290. https://doi.org/10.1007/BF02214232

Catsadorakis G, Paragamian K (2007) Inventory of the wetlands of the Aegean Islands: Identity, ecological status and threats.World Wildlife Fund for Nature – WWF Greece, Athens, 392 pp. [in Greek]

Cattaneo C, Grano M (2013) Note sul paesaggio vegetale e sulla flora vascolare estiva dell'isola egea di Skiathos e delle sue due isola circonvicine Tsougria e Aspronisо (Sporadi settentrionali, Grecia). Annali - Fondazione Museo Civico di Rovereto 29(2014): 243–288.

Cattaneo A (1997) L`erpetofauna dell`isola greca di Skiathos (Sporadi settentrionali). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 136: 145–156.

Cattaneo A (1998) Gli anfibi e i rettili delle isole greche di Skyros, Skopelos e Alonissos (Sporadi settentrionali). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale 139(2): 127–149.

Cattaneo A (1999) Variabilita e sottospecie di *Elaphe quatuorlineata* (Lacépède) nelle piccole isole Egee (Serpentes: Colubridae). Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale 140(1): 119–139.

Cattaneo A (2003) Note erpetologiche sulle isole egee di Lesvos, Chios e Samos. Bollettino del Museo civico di storia naturale di Venezia 54: 95–116.

Cattaneo A (2010) Note eco-morfologiche su alcune specie ofidiche egee, con particolare riferimento alle popolazioni delle Cicladi centro-orientali (Reptilia). Naturalista siciliano, S. IV, XXXIV (3–4): 319–350.

Cattaneo A (2021) Variabilitá di *Vipera ammodytes* (Linnaeus, 1758) (*Reptilia Viperidae*) in alcune isole egee, con descrizione di *Vipera ammodytes buccholzi* subsp. nova. Naturalista siciliano, S. IV, XLV (1–2): 119–152.

Cheng W (2015) Impact of livestock grazing on ecosystem services in a Mediterranean ecosystem. MS Thesis, University of Michigan, Ann Arbor.

Chondropoulos BP (1986) A checklist of the Greek reptiles, I. The lizards. Amphibia-Reptilia 7: 217–235. https://doi.org/10.1163/156853886X00028

Chondropoulos BP (1989) A checklist of Greek reptiles, II. The Snakes. Herpetozoa 2(1/2): 3–36.

Crucitti P, Tringali L (1987) Alcune caratteristiche dell erpetofauna Ellenica (Amphibia-Reptilia). In: Crucitti P (Ed.) Atti del Convegno sul Tema Zoologia Ellenica (Roma, 17.5.1986). Societa Romana di Scienze Naturali, Roma, 4–19.

Cyrén O (1935) Herpetologisches vom Balkan. Blätter für Aquarien- und Terrarien-Kunde 46(6): 129–135.

Cyrén O (1941) Beiträge zur Herpetologie der Balkanhalbinsel. Mitteilungen aus den Königlich Naturwissenschaftlichen Instituten in Sofia 14: 36–152.

Daftsios T, Iakovidis D, Gogolos N, Sagonas K (2024) First record of *Hemidactylus turcicus* (Linnaeus, 1758) from Piperi Island, Northern Sporades, Greece. Herpetozoa 37: 227–229. https://doi.org/10.3897/herpetozoa.37.e122349

Dermitzakis MD (1990) Paleogeography, geodynamic processes and event stratigraphy during the late Cenozoic of the Aegean area. Academia Nazionale de Lincei 85: 263–288.

Diamond J (1975) Assembly of species communities. In: Cody L, Diamond J (Eds) Ecology and Evolution of Communities. Belknap Press, Cambridge, 342–444.

Donihue C, Brock KM, Foufopoulos J, Herrel A (2015) Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. Functional Ecology 30(4): 566–575. https://doi.org/10.1111/1365-2435.12550

Ergül Kalaycı T, Kurtul D, Gül Ç, Tosunoğlu M (2023) Genetic status of *Hemidactylus turcicus* (Linnaeus, 1758) from Çanakkale (Turkey). Biology Bulletin 50(5): 773–783. https://doi.org/10.1134/S106235902360188X

Ferentinos GC (1972) The geology-petrology of the island of Skiathos. PhD thesis, University of Patras, Patras, Greece.

Foufopoulos J, Ives A (1999) Reptile extinctions on land-bridge islands: life history attributes and vulnerability to extinction. American Naturalist 153(1): 1–125. https://doi.org/10.1086/303149

Foufopoulos J, Kilpatrick M, Ives A (2011) Holocene climate change and elevated extinction rates of northern reptile species from Mediterranean islands. American Naturalist 177(1): 119–129. https://doi.org/10.1086/657624

Foufopoulos J, Zhao Y, Brock KM, Pafilis P, Valakos E (2023) Predation risk, and not shelter or food availability, as the main determinant of reproduction investment in island lizards. Animals 13(23): 3689. https://doi.org/10.3390/ani13233689

Frör E (1978) Intraspecific differentiation of the green lizards *Lacerta trilineata* and *Lacerta viridis* of Greece. Biologia Gallo-Hellenica, 331–334.

Ginalis AA (2018) Insularity and identity in the Northern Sporades islands: the question of Roman policy in central Greece. In: Kouremenos A (Ed.) Insularity and Identity in the Roman Mediterranean. Oxbow Books, Oxford, 65–77. https://doi.org/10.2307/j.ctvh1dmsx.8

Gizicki Z, Tamez V, Galanopoulou A, Avramidis P, Foufopoulos J (2018) Long-term effects of feral goats (*Capra hircus*) on Mediterranean island communities: results from whole island manipulations. Biological Invasions 20: 1537–1552. https://doi.org/10.1007/s10530-017-1645-4.

Grano M, Cattaneo C, Cattaneo A (2013) First record of *Hierophis gemonensis* (Laurenti, 1768) (Reptilia Serpentes Colubridae) in the Aegean island of Tsougriá, Northern Sporades, Greece. Biodiversity Journal 4(4): 553–556.

Grillitsch H, Grillitsch B (1999) *Telescopus fallax* (Fleischmann 1831) – Europäische Katzennatter. In: Böhme W (Ed.) Handbuch der Reptilien und Amphibien Europas. Bd. 3/IIA: Schlangen II, Serpentes II: Colubridae 2 (Boiginae, Natricinae). Aula, Wiebelsheim, 757–788.

Grillitsch H, Tiedemann F (1984) Zur Herpetofauna der griechischen Inseln Kea, Spanopoula, Kithnos, Sifnos, Kitriani (Cycladen), Alonissos und Piperi (Nördliche Sporaden). Annalen des Naturhistorischen Museums Wien (B) 86: 7–28.

Gruber UF (1971) Die Inselpopulationen der Cycladen-Eidechse (*Lacerta erhardii*) in der Ägäis. Opera Botanica 30: 69–79.

Gruber UF (1974) Zur Taxonomie und Ökologie der Reptilien von der Insel Antikythira. Salamandra 10 (1): 31–41.

Gruber UF (1986) *Podarcis erhardii* (Bedriaga 1876) - Ägäische Mauereidechse. In: Böhme W (Ed.) Handbuch der Reptilien und Amphibien Europas. Bd. 2 / II, Echsen III (*Podarcis*), Aula, Wiesbaden, 25–49.

Gruber UF, Fuchs D (1977) Die Herpetofauna des Paros-Archipels (Zentral-Ägäis). Salamandra 13: 60–77.

Gruber UF, Schultze-Westrum TF (1971) Zur Taxonomie und Ökologie der Cycladen-Eidechse (*Lacerta erhardii*) von den Nördlichen Sporaden. Bonner Zoologische Beiträge 22: 101–130. https://doi.org/10.1002/fedr.4910820202

Hailey A, Willemsen RE (2003) Changes in the status of tortoise populations in Greece 1984–2001. Biodiversity and Conservation 12: 991–1011. https://doi.org/10.1023/A:1022815120619

Harris I, Osborn T, Jones P, Lister D (2020) Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. Scientific Data 7: 109. https://doi.org/10.1038/s41597-020-0453-3 [Climate Change Knowledge Portal, Greece. https://climateknowledgeportal.worldbank.org/country/greece/climate-data-historical]

Henle K (1993) *Coluber gemonensis* (Laurenti 1768) – Balkanzornnatter. In: Böhme W (Ed.) Handbuch der Reptilien und Amphibien Europas; Schlangen (Serpentes) vol. 3/I. Aula, Wiesbaden, 97–110.

Hutter CP, Hau G (2001) Ägäis: Nördliche Sporaden – Natur entdecken und erleben. Radolfzell (Weitbrecht) EuroNatur-Erlebnisführer 176 pp.

Iliadou E, Bazos I, Kougioumoutzis K, Karadimous E, Kokkoris I, Panitsa M, Raus T, Strid A, Dimopoulos P (2020) Taxonomic and phylogenetic diversity patterns in the Northern Sporades islets complex (west Aegean, Greece). Plant Systematics and Evolution 306: 28. https://doi.org/10.1007/s00606-020-01660-0

Itescu Y, Schwarz R, Meiri S, Pafilis P (2017) Intraspecific competition, not predation, drives lizard tail loss on islands. Journal of Animal Ecology 86(1): 66–74. https://doi.org/10.1111/1365-2656.12591

Itescu Y, Schwarz R, Donihue C, Slavenko A, Roussos S, Sagonas K, Valakos E, Foufopoulos J, Pafilis P, Meiri S (2018) Inconsistent patterns of body size evolution in co-occurring island reptiles. Global Ecology and Biogeography 27(5): 538–550. https://doi.org/10.1111/geb.12716

Jacobshagen V, Wallbrecher E (1984) Pre-Neogene nappe structure and metamorphism of the North Sporades and the southern Pelion peninsula. Geological Society, London, Special Publications 17(1): 591–602. https://doi.org/10.1144/GSL.SP.1984.017.01.46

Kalb S (2021) Climatic and environmental drivers of extinction in Mediterranean island reptiles since the height of the last Ice Age. MS Thesis, University of Michigan, Ann Arbor, Michigan, United States.

Kamari G, Phitos D, Snogerup B, Snogerup S (1988) Flora and vegetation of Yioura, N Sporades, Greece. Willdenowia 17: 59–85.

Kasapidis P, Magoulas A, Mylonas M, Zouros E (2005) The phylogeography of the gecko *Cyrtopodion kotschyi* (Reptilia: Gekkonidae) in the Aegean archipelago. Molecular Phylogenetics and Evolution 35 (3): 612–623. https://doi.org/10.1016/j.ympev.2005.02.005

Kalogiannis S (2020) A concolor morph in *Podarcis erhardii ruthveni* (Werner, 1930) from Alonissos, Greece. Parnassiana Archives 8: 121–123.

Kalogiannis S (2021) Cases of melanism in *Dolichophis caspius* (Gmelin, 1789) (Squamata, Colubridae) from Greece and a new distribution record. Parnassiana Archives 9: 19–22.

Kalogiannis S, Stefanopoulos P (2023) First report on the herpetofauna of Palaio Trikeri island (Pagasetic gulf, Greece). Ecologia Balkanica 15(2): 107–111.

Kizos T, Spilanis I, Koulouri M (2007) The Aegean Islands: a paradise lost? In: Pedroli B, Van Doorn A, De Blust G, Paracchini ML, Wascher D, Bunce F (Eds) Europe's Living Landscapes: Essays exploring our identity in the countryside. Landscape Europe, Wageningen / KNNV Publishing, Zeist, 332—349. [ISBN: 9789004278073, 333] https://doi.org/10.1163/9789004278073_021

Kochva E (1965) The development of the venom gland in the opisthoglyph snake *Telescopus fallax* with remarks on *Thamnophis sirtalis* (Colubridae, Reptilia). Copeia 1965: 147–154. https://doi.org/10.2307/1440716

Kock D, Storch G (1979) *Testudo marginata* (Schoepff 1792) auf den nördlichen Sporaden, Ägäis. Salamandra 15(2): 101–105.

Konaxis I (2020) Alonissos Island and the Northern Sporades Marine National Park as a strategic socio-economic node for the culture of the Aegean Sea. American Research Journal of Humanities and Social Science 3(10): 49–53.

Kornilios P, Thanou E, Lymberakis P, Ilgaz Ç, Kumlutaş Y, Leaché A (2020) A phylogenomic resolution for the taxonomy of Aegean green lizards. Zoologica Scripta 49: 14–27. https://doi.org/10.1111/zsc.12385

Kornilios P, Kyriazi P, Poulakakis N, Kumlutaş Y, Ilgaz Ç, Mylonas M, Lymberakis P (2010) Phylogeography of the ocellated skink *Chalcides ocellatus* (Squamata, Scincidae), with the use of mtDNA sequences: A hitch-hiker's guide to the Mediterranean. Molecular Phylogenetics and Evolution 54(2): 445–456. https://doi.org/10.1016/j.ympev.2009.09.015

Kossoff A (2023) Assessment of Introduced European Rabbits (*Oryctolagus cuniculus*) in Island Ecosystems in the Mediterranean. MS Thesis, University of Michigan, Ann Arbor, Michigan, United States. https://doi.org/10.3390/d16040244

Kotsakiozi P, Jablonski D, Ilgaz C, Kumlutas Y, Avci A, Meiri S, Itescu Y, Kukushkin O, Gvoždík V, Scillitani G, Roussos S, Jandzik D, Kasapidis P, Lymberakis P, Poulakakis N (2018) Multilocus phylogeny and coalescent species delimitation in Kotschy's gecko, *Mediodactylus kotschyi*: hidden diversity and cryptic species. Molecular Phylogenetics and Evolution 125: 177–187. https://doi.org/10.1016/j.ympev.2018.03.022

Krawczyk E, Hedman H, Pafilis P, Bergen K, Foufopoulos J (2019) Effects of touristic development on Mediterranean island wildlife. Landscape Ecology 34: 2719–2734. https://doi.org/10.1007/s10980-019-00917-5

Legakis A (2004) Survey of the terrestrial biodiversity of the National Marine Park of Alonnisos – Northern Sporades. Final Report Protection of the Environment and Sustainable Development Programme. Athens (Ministry of Environment, Zoological Museum, Department of Biology, University of Athens). [in Greek]

Li B, Belasen A, Pafilis P, Bednekoff P, Foufopoulos J (2014) Effects of feral cats on the evolution of anti-predator behaviours in island reptiles: insights from an ancient introduction. Proceedings of the Royal Society B: Biological Sciences 281: 20140339.

Lowe MR (1999) Notes sur les orchidées des Sporades du Nord (Nomos Magnesia, Grèce). Les Naturalistes Belges 80 (Orchid 12): 155–172.

Lymberakis P, Pafilis P, Poulakakis N, Sotiropoulos K, Valakos ED, Sfenthourakis S (2018) The amphibians and reptiles of the Aegean sea. Biogeography and Biodiversity of the Aegean. In honor of Prof. Moysis Mylonas, 169–189.

Madden I, Brock KM (2018) An extreme record of cannibalism in *Podarcis erhardii mykonensis* (Reptilia: Lacertidae) from Siros island, Cyclades, Greece. Herpetology Notes 11: 291–292.

Masseti M (2012) Atlas of terrestrial mammals of the Ionian and Aegean Islands. De Gruyter, Berlin/Boston, 302 pp. https://doi.org/10.1515/9783110254587

Mayer W, Tiedemann F (1980) Elektrophoretische Untersuchungen an europäischen Arten der Gattungen *Lacerta* und *Podarcis*; I. Die *Podarcis*-Formen der griechischen Inseln Milos und Skiros. Zeitschrift für Zoologische Systematik und Evolutionsforschung 18: 147–152. https://doi.org/10.1111/j.1439-0469.1980.tb00735.x

Medina FM, Bonnaud E, Vidal E, Tershy BR, Zavaleta ES, Donlan CJ, Keitt BS, Le Corre M, Horwath SV, Nogales M (2011) A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology 17: 3503–3510. https://doi.org/10.1111/j.1365-2486.2011.02464.x

Mertens R, Wermuth H (1960) Die Amphibien und Reptilien Europas. W. Kramer, Frankfurt am Main XI, 264 pp.

Ministry of Environment, Physical Planning and Public Works (2002) Special environmental study of the protected area of the National Marine Park of Alonissos, Northern Sporades, Athens. [in Greek]

Moravec J, Kratochvil L, Amr Z, Jandzik D, Šmíd J, Gvoždik V (2011) High genetic differentiation within the *Hemidactylus turcicus* complex (Reptilia: Gekkonidae) in the Levant, with comments on the phylogeny and systematics of the genus. Zootaxa 2894(1): 21–38. https://doi.org/10.11646/zootaxa.2894.1.2

Muñoz M, Losos J (2018) Thermoregulatory behavior simultaneously promotes and forestalls evolution in a tropical lizard. American Naturalist 191(1): 15–26. https://doi.org/10.1086/694779

Myers N, Mittermeier R, Mittermeier C, da Fonseca G, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. https://doi.org/10.1038/35002501

National Statistical Service of Greece (2011) Detailed census results 2011 (xls 2,7 MB). [in Greek]

Wikipedia: Sporades [in Greek] https://el.wikipedia.org/wiki/Σποράδες

Nossan H (2023) Biodiversity implications of agricultural terrace abandonment in a Mediterranean landscape. MS Thesis, University of Michigan, Ann Arbor, United States.

Ondrias JC (1968) Liste des Amphibiens et des Reptiles de Grece. Biologia Gallo-Hellenica 1: 11–135.

Osorio YM, Ales RG, Machado EA, Acosta JC (2024) Impact of vineyards on habitat's thermal conditions and functional traits of a lizard in the central Monte Desert, Argentina. Journal of Arid Environments 221: 105143. https://doi.org/10.1016/j.jaridenv.2024.105143

Pafilis P, Anastasiou I, Sagonas K, Valakos E (2013) Grazing by goats on islands affects the populations of an endemic Mediterranean lizard. Journal of Zoology 290(4): 255–264. https://doi.org/10.1111/jzo.12032

Pafilis P, Meiri S, Foufopoulos J, Valakos E (2009) Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaffen 96: 1107–1113. https://doi.org/10.1007/s00114-009-0564-3

Papanastasis VP, Mantzanas K, Dini-Papanastasi O, Ispikoudis I (2009) Traditional agroforestry systems and their evolution in Greece. Agroforestry in Europe: current status and future prospects 89–109. https://doi.org/10.1007/978-1-4020-8272-6_5

Passarge H (2019) Insel-Idylle und *Podarcis erhardii ruthveni* (Werner 1930) auf Alonnisos, nördliche Sporaden, Griechenland. Eidechse 30(1): 24–35.

Patharkar T, Van Passel L, Brock K (2022) Eat or be eaten? An observation of *Podarcis erhardii* consuming *Scolopendra cingulata* from Andros Island, Cyclades, Greece. Herpetozoa 35: 209–212. https://doi.org/10.3897/herpetozoa.35.e94006

Plettenberg-Laing A, Mee G (2020) Remarks on the diet of *Dolichophis caspius* (Gmelin, 1789) from Greece. Herpetology Notes 13: 989–991.

Pogorevc N, Dotsev A, Upadhyay M, Sandoval-Castellanos E, Hanneman E, Simčič M, Antoniou A, Papachristou D, Koutsouli P, Rahmatalla S, Brockmann G, Sölkner J, Burger P, Lymberakis P, Poulakakis N, Bizelis I, Zinovieva N, Horvat S, Medugorac I (2024) Whole-genome SNP genotyping unveils ancestral and recent introgression in wild and domestic goats. Molecular Ecology 33(1): e17190. https://doi.org/10.1111/mec.17190

Poulakakis N, Lymberakis P, Valakos E, Zouros E, Mylonas M (2005) Phylogenetic relationships and biogeography of *Podarcis* species from the balkan peninsula, by bayesian and maximum likelihood analyses of mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 37(3): 845–857. https://doi.org/10.1016/j.ympev.2005.06.005

Rato C, Carranza S, Harris DJ (2011) When selection deceives phylogeographic interpretation: The case of the Mediterranean house gecko,

Hemidactylus turcicus (Linnaeus, 1758). Molecular Phylogenetics and Evolution 58(2): 365–373. https://doi.org/10.1016/j.ympev.2010.12.004

Reiser O (1905) Materialien zu einer Ornis balcanica (Vol. 3). A Holzhausen (Ed). Karl Gerold Sohn Publishers, Vienna.

Roca V, Foufopoulos, J, Valakos E, Pafilis P (2009) Parasitic infracommunities of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Sauria): isolation and impoverishment in small island populations. Amphibia-Reptilia 30(4): 493–503. https://doi.org/10.1163/156853809789647176

Rodda GH, Dean-Bradley K (2002) Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography, 29: 623–632. https://doi.org/10.1046/j.1365-2699.2002.00711.x

Rohling EJ, Foster GL, Grant KM, Marino G, Roberts AP, Tamisiea ME, Williams F (2014) Sea-level and deep-sea temperatures variability over the past 5.3 million years. Nature 508: 477–482. https://doi.org/10.1038/nature13230

Roussos S (2015) Integrative evolutionary biogeography of the nose-horned viper (Viperidae: Squamata) in the Cycladic Archipelago and continental Greece. PhD Dissertation, Texas Tech University, Lubbock.

Runemark A, Sagonas K, Svensson E (2015) Ecological explanations to island gigantism: dietary niche divergence, predation, and size in an endemic lizard. Ecology 96(8): 2077–2092. https://doi.org/10.1890/14-1996.1

Sampson A (2006) The prehistory of the Aegean. Atrapos Ed., Athens.

Schultze-Westrum T (1961) Beobachtungen an Eleonorenfalken (*Falco eleonorae*). Anzeiger der Ornithologischen Gesellschaft Bayern 6: 84–86.

Semegen S (2018) Predation pressure as a determinant of locomotor performance: lizards run slower on islands without predators. MS Thesis, University of Michigan, Ann Arbor, Michigan, United States.

Sigg H (1984) Anspruchsvolle Schönheit. Anforderungen von *Elaphe situla* an Lebensraum und Terrarium. Herpetofauna, Weinstadt 6: 11–20.

Spangenberg A (2005) Mehr als Meer und Mönchsrobbe – der Meeresnationalpark Nördliche Sporaden. Euronatur, Radolfzell 4: 12–13.

Speybroeck J, Beukema W, Bok B, Van der Voort J, Velikov I (2021) Field Guide to the Amphibians and Reptiles of Britain and Europe. Bloomsbury Publishing, London, 432 pp.

Stadler S, Brock K, Bednekoff P, Foufopoulos J (2023) More and bigger lizards reside on islands with more resources. Journal of Zoology 319(3): 163–174. https://doi.org/10.1111/jzo.13036

Strachinis I, Artavanis D (2017) Additions to the known herpetofauna of the Island of Ithaki, Ionian Sea, Greece. Herpetozoa 30 (1/2): 64–66.

Strachinis I, Roussos SA (2016) Terrestrial herpetofauna of Limnos and Agios Efstratios (Northern Aegean, Greece), including new species records for *Malpolon insignitus* (Geoffroy SaintHilaire, 1827) and *Pelobates syriacus* Boettger, 1889. Herpetology Notes 9: 237–248.

Strachinis I (2022) First insights on the herpetofauna of Ammouliani island, Greece. Ecologia Balkanica 14(2): 199–203.

Stille B, Stille M (2015) The herpetofauna of Mathraki, Othonoi and Erikoussa, Diapontia islets, Greece. Herpetozoa 28(3/4): 193–197.

Tiedemann F, Mayer W (1980) Ein Beitrag zur systematischen Stellung der Skyroseidechse. Annalen des Naturhistorischen Museums in Wien 83: 543–546.

Valakos ED, Pafilis P, Sotiropoulos K, Lymberakis P, Maragou P, Foufopoulos J (2008) The Amphibians and Reptiles of Greece. Chimaira, Frankfurt am Main, 563 pp.

Watson G (1962) Notes on copulation and distribution of Aegean land tortoises. Copeia 1962: 317–321. https://doi.org/10.2307/1440897

Weber C (2014) Ecological impacts of invasive rat removal on Mediterranean sea islands. MS Thesis, University of Michigan, Ann Arbor, Michigan, United States.

Werner F (1929) Zoologische Forschungsreise nach den Jonischen Inseln und dem Peloponnes. V. Teil: Reptilia, Amphibia, Orthoptera, Embidaria und Scorpiones. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien, Abteilung 1, 138: 471–485.

Werner F (1930) Contribution to the knowledge of the reptiles and amphibians of Greece especially the Aegean islands. Occasional papers of the Museum of Zoology, University of Michigan 211: 1–47.

Werner F (1933) Ergebnisse einer zoologischen Studien- und Sammelreise nach den Inseln des Agäischen Meeres. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien, Abteilung 1, 142(3/4): 103–133.

Werner F (1938a) Die Amphibien und Reptilien Griechenlands. Zoologica, Stuttgart, 116 pp.

Werner F (1938b) Ergebnisse der 8. zoologischen Forschungsreise nach Griechenland (Euböa, Tinos, Skiathos, Thasos usw.). Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 147: 151–163.

Wettstein O (1953) Herpetologia aegaea. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 65: 651–833. https://doi.org/10.1007/978-3-662-25591-9_1

Wettstein O (1957a) Nachtrag zu meiner Herpetologia aegaea. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien 166: 123–164.

Wettstein O (1957b) *Lacerta erhardii scopelensis* Cyrén, 1941. - In: Nachtrag zu meiner Herpetologia aegaea. – Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien, Abteilung 1, 166(3/4): 138–140, 156.

Wettstein O (1957c) *Lacerta erhardii ruthveni Werner*. - In: Nachtrag zu meiner Herpetologia aegaea. – Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien, Abteilung 1, 166(3/4): 140–142, 156.

Zakkak S, Halley JM, Akriotis T, Kati V (2015) Lizards along an agricultural land abandonment gradient in Pindos Mountains, Greece. Amphibia-Reptilia 36(3): 253–264. https://doi.org/10.1163/15685381-00003002

Appendix 1

Table A1. Photographic records from iNaturalist or citizen photographers provided to the authors.

Photographer	Date	Species	Island	Additional Information (URL, coordinates, location description etc.)
Theodora Tsimpo	7/2009	*P. apodus*	Skopelos	N/A
Genevieve Leaper	5/29/2020	*E. quatuorlineata*	Kyra Panagia	https://www.inaturalist.org/observations/49866458
Luca di Cianni	3/8/2018	*T. fallax*	Skopelos	39.126064°N, 23.746339°E
Vassilis Malamatenios	8/25/2020	*T. fallax*	Peristera	Bay of Vasiliko
Konstantina Malamateniou	11/29/2020	*Z. situla*	Alonnisos	39.233056°N, 23.953889°E

Table A2. Local names of some reptile species in the Sporades.

Binomial name	Greek common name	Local name(s)
Ablepharus kitaibelii	Αβλέφαρος	Ήλιος (*Ìlios*) (Alonnisos) - meaning 'sun'
Lacerta trilineata	Τρανόσαυρα	Αγκουστέρα (*Angustéra*) (Skiathos)
Podarcis erhardii	Αιγαιόσαυρα	Ακουστέρα (*Akustéra*) (Alonnisos)-'ου' not audible
Dolichophis caspius	Έφιος	Δεντρογαλιά (*Thendrogaliá*) (Alonnisos)
Elaphe quatuorlineata	Λαφιάτης	Δενδρίτης (*Thendreétis*) (Skiathos), Τυφλίτης (*Tifleétis*)(Alonnisos)
Malpolon insignitus	Σαπίτης	Δεντρογαλιά, Σαπίτης (*Dendrogaliá*, *Sapeétis*)
Platyceps najadum	Σαΐτα	Σαϊτάρι (*Saitári*)
Telescopus fallax	Αγιόφιδο	Αστρίτης (*Astreétis*)
Zamenis situla	Σπιτόφιδο	Αστρίτης (*Astreétis*)
Vipera ammodytes	Οχιά	Οχιά or Αστρίτης (*Ochiá*) - used to differentiate between color morphs
Testudo marginata	Κρασπεδωτή χελώνα	Αχελώνα (*Achelóna*) (Alonnisos)

Table A3. List of islands/islets and their alternative names, with abbreviations as used in Fig. 1. and Tables 1, 2.

Name used here	Other names	Abbreviation	Coordinates
Skiathos	–	–	39.178667°N, 23.469917°E
Kastronisia	–	KST	39.212611°N, 23.461528°E
Aspronisi	Aspro	ASP	39.171389°N, 23.520944°E
Arkos	Arko, Arkaki	ARK	39.15075°N, 23.517806°E
Repi	Repio, Repion, Trypiti	REP	39.147222°N, 23.528167°E
Maragos	Marangos, Maranko	MAR	39.151278°N, 23.500361°E
Daskalonisi	Daskalio, Daskalos	DAK	39.160917°N, 23.494944°E
Tsougria	Tsougrias, Sugria	TSA	39.122667°N, 23.499472°E
Tsougkriaki	Mikrosugria	TSI	39.125083°N, 23.4815°E
Paximadi	Paximada	PAX	39.14725°N, 23.591861°E
Plevro	Plero, Klima	PLE	39.135694°N, 23.619639°E
Kassidis (Skopelos)	Kassida	KAS	39.129833°N, 23.614333°E
Strongylo (Skop)	Stroggylo	STR	39.113778°N, 23.626028°E
Dasia	Dhasia, Dasa	DAS	39.116639°N, 23.637639°E
Skopelos	–	–	39.131833°N, 23.683806°E
Agios Georgios	Agios Giorgos	AGG	39.135139°N, 23.80175°E
Mikronisi	Mikro	MIK	39.14125°N, 23.809778°E
Alonnisos	Liadromia, Chiliodromia, Ikos	–	39.198389°N, 23.902167°E
Manolas	Manola	MAN	39.201556°N, 23.862611°E
Kokkinokastro	Kokkinonisi	KOK	39.161111°N, 23.904361°E
Peristera	Xero, Xeronisi, Peristeri	PER	39.186°N, 23.973611°E
Lechousa	Lykoremma, Lykourina	LEO	39.228556°N, 23.998917°E
Megalos Adelphos	Adelfi, Megalo Adelfi	MEA	39.111694°N, 23.979361°E
Mikros Adelphos	Adelfopoula, Mikro Adelfi	MIA	39.125639°N, 23.988111°E
Gaidaronisi	Gaidaros, Gaidares	GAI	39.067611°N, 23.951139°E
Prasso	Prassonisi, Paraos, Parausa	PRA	39.072306°N, 24.095972°E
Strongylo	Stroggylo, Kyriagos	KYR	39.082833°N, 24.086306°E
Skantzoura	–	–	39.080028°N, 24.110222°E
Kassidis (Skantzoura)	Kassida	KSD	39.106528°N, 24.091722°E
Lachanou	–	LAC	39.104611°N, 24.096222°E
Polemika	Polemiko	POL	39.101389°N, 24.100167°E
Skandili	Skantili, Korakas	SKA	39.048056°N, 24.08125°E
Mikroskandili	Kyriakos	MKS	39.054111°N, 24.082861°E
Korakas	Korakonisi, Prasouda	KOR	39.035°N, 24.061361°E
Kyra Panagia	Pelagonisi, Pelagos, Ephthyros	–	39.330222°N, 24.073056°E
Agios Petros	–	AGP	39.321722°N, 24.055028°E
Pelerissa	Sphagru, Fagrou	PEL	39.313361°N, 24.037722°E
Melissa	–	MEL	39.292694°N, 24.090139°E
Sfika	Sphiga	SFI	39.359861°N, 24.078833°E
Pappous	Papous, Papu	PAP	39.353972°N, 24.121°E
Koumbi	Strongyli	KOY	39.350278°N, 24.127889°E
Grammeza	Gramsa, Prasso	GRA	39.342306°N, 24.139139°E
Gioura	Gioura, Yioura, Gerontia	–	39.388528°N, 24.170611°E
Psathoura	Psathura	PSA	39.498472°N, 24.179778°E
Mikropsathoura	Psathonisi, Myga	MPS	39.482583°N, 24.181444°E
Piperi	–	–	39.348333°N, 24.324333°E